SHOUT
SHARE
IT

MBL/WHOI
0 0301 0033345 0

A TEXT-BOOK OF BOTANY

MACMILLAN AND CO., Limited
LONDON · BOMBAY · CALCUTTA
MELBOURNE

THE MACMILLAN COMPANY
NEW YORK · BOSTON · CHICAGO
ATLANTA · SAN FRANCISCO

THE MACMILLAN CO. OF CANADA, Ltd.
TORONTO

S481

A

TEXT-BOOK OF BOTANY

BY

DR. EDUARD STRASBURGER
PROFESSOR IN THE UNIVERSITY
OF BONN

DR. FRITZ NOLL
PROFESSOR IN THE AGRICULTURAL ACADEMY
OF POPPELSDORF AND IN THE UNIVERSITY OF BONN

DR. HEINRICH SCHENCK
PROFESSOR IN THE TECHNICAL
ACADEMY OF DARMSTADT

DR. GEORGE KARSTEN
PROFESSOR IN THE UNIVERSITY
OF BONN

THIRD ENGLISH EDITION

REVISED WITH THE EIGHTH GERMAN EDITION BY

W. H. LANG, M.B., D.Sc.
LECTURER IN BOTANY, UNIVERSITY OF GLASGOW

MARINE BIOLOGICAL LABORATORY
LIBRARY
WOODS HOLE, MASS.

WITH 779 ILLUSTRATIONS, IN PART COLOURED

MACMILLAN AND CO., LIMITED
ST. MARTIN'S STREET, LONDON
1908

N497(1)

First English Edition, 1898
Second English Edition, 1903
Third English Edition, 1908

2389

PREFATORY NOTE

THE first edition of the English translation of this text-book was the work of Dr. H. C. Porter, Assistant Instructor of Botany, University of Pennsylvania. The proofs of this edition were revised by Professor Seward, M.A., F.R.S. The second English edition was based upon Dr. Porter's translation, which was revised with the fifth German edition. The present edition has been similarly revised throughout with the eighth German edition. Such extensive changes, including the substitution of a completely new section on Phanerogamia, have however been made in the latter that it seemed advisable to give in outline the history of the English translation instead of retaining Dr. Porter's name on the title page.

The official plants mentioned under the Natural Orders are those of the British Pharmacopœia instead of those official in Germany, Switzerland, and Austria, which are given in the original. In making this alteration I have consulted *Materia Medica and Therapeutics*, by J. Mitchell Bruce, M.A., LL.D., M.D.

The fact that a considerable portion of the original has been rewritten, has necessitated the preparation of a new and extended index. I am indebted to my friend, Mr. F. Tidd Pratt, for assistance in this.

WILLIAM H. LANG.

GLASGOW, *February* 1908.

MARINE BIOLOGICAL LABORATORY
WOODS HOLE
LIBRARY
MASS.

MARINE BIOLOGICAL LABORATORY
LIBRARY
MASS.

CONTENTS

PAGE
INTRODUCTION 1

PART I. GENERAL BOTANY

SECTION I. MORPHOLOGY

I. EXTERNAL MORPHOLOGY

The development of form in the plant kingdom 11
The shoot 18
  Metamorphosis of the shoot 23
  Leaves 30
  Metamorphosis of leaves 43
The root 45
  Metamorphosis of the root 48
Members of independent origin 49

II. INTERNAL MORPHOLOGY

(Histology and Anatomy)

The cell 52
  Protoplasm 54
  Cell wall 63
  Inclusions of the protoplasm 73
  Cell sap 79
  Ontogeny of the cell 80
Cell fusions 93
Tissues 97
Primary tissues 100
Secondary tissues 127
Regeneration 151
Phylogeny of the internal structure 152
Ontogeny of the internal structure 154
Structural deviations 165

SECTION II. PHYSIOLOGY

PAGE
Physical and vital properties. General conditions of life . . . 172
The stability of the plant body 178
Nutrition 186
Respiration 239
Growth 247
The phenomena of movement 263
Reproduction 296

PART II. SPECIAL BOTANY

SECTION I. CRYPTOGAMS

A Mg THALLOPHYTA 329
  Bacteria 331
  Cyanophyceae 337
  Flagellata 339
  Myxomycetes 340
  Peridineae 342
  Conjugatae 344
  Diatomeae 347
  Heterocontae 351
  Chlorophyceae 353
  Characeae 363
  Phaeophyceae 365
  Rhodophyceae 373
  Phycomycetes 378
  Eumycetes 386
  Lichenes 415
F Mg BRYOPHYTA 421
  Hepaticae 425
  Musci 431
C Mg PTERIDOPHYTA 438
  Filicinae 443
  Eusporangiatae 443
  Leptosporangiatae 445
  Equisetinae 455
  Lycopodinae 458
D FOSSIL CRYPTOGAMS 465

SECTION II. PHANEROGAMIA

TRANSITION FROM THE CRYPTOGAMS TO THE PHANEROGAMS . . 471
TABLE OF CLASSES, ORDERS, AND FAMILIES OF PHANEROGAMS . . 478
E GYMNOSPERMAE 480
  Development of the sexual generation 480
  Cycadinae 484

PAGE
- Ginkgoinae 488
- Coniferae 489
- Gnetinae 498

FOSSIL GYMNOSPERMS 500

cl ANGIOSPERMAE 501
- The angiospermic flower 501
- Inflorescence 509
- Sexual generation 513
- Fruit 519

Scl MONOCOTYLAE 521
- Helobiae 522
- Glumiflorae 524
- Spadiciflorae 530
- Enantioblastae 536
- Liliiflorae 536
- Scitamineae 546
- Gynandrae 548

Scl DICOTYLAE 551
- Choripetalae 552
  - Piperinae 552
  - Juglandiflorae 554
  - Saliciflorae 555
  - Querciflorae 556
  - Urticinae 563
  - Centrospermae 566
  - Polycarpicae 571
  - Rhoeadinae 585
  - Insectivorae 591
  - Saxifraginae 591
  - Rosiflorae 593
  - Leguminosae 599
  - Gruinales 610
  - Tricoccae 615
  - Sapindinae 618
  - Frangulinae 621
  - Columniferae 623
  - Cistiflorae 627
  - Passiflorinae 630
  - Opuntinae 630
  - Thymelaëinae 631
  - Myrtiflorae 631
  - Umbelliflorae 635
  - Hysterophyta 643

H SYMPETALAE 645
- Pentacyclicae 645
  - Ericinae 645
  - Diospyrinae 646
  - Primulinae 647
- Tetracyclicae 649
  - Contortae 649

PAGE
Tubiflorae 656
Personatae 661
Rubiinae 668
Campanulinae 675
Aggregatae 679
FOSSIL ANGIOSPERMS 688

INDEX OF LITERATURE 691
SYSTEMATIC INDEX OF OFFICIAL AND POISONOUS PLANTS . . . 717
INDEX 721

INTRODUCTION

It is customary to place all living beings in either the animal or vegetable kingdoms, but in reality a sharp boundary line between animals and plants first becomes possible when they exhibit a complicated structure. In those of more simple organisation all distinctions disappear, and it becomes difficult to define the exact limits of Botany and Zoology. This, in fact, could scarcely be otherwise, as all the processes of life, in both the animal and vegetable kingdoms, are dependent on the same substance, protoplasm. With more complicated organisation, the specific differences increase, and the characteristics distinguishing animal from vegetable life become more obvious. For the present, it must be confessed, the recognition of an organism, as an animal or a plant, is dependent upon its correspondence with an abstract idea of what a plant or animal should be, based on certain points of agreement between the members of each class. A satisfactory basis for the separation of all living organisms into the categories of animals or plants can only be obtained when it is shown that all organisms distinguished as animals are in reality genetically connected, and that a similar connection exists between all plants. The proof of this can only be arrived at through the THEORY OF EVOLUTION.

From the study of the fossil remains and impressions of animals and plants, it has been established that in former epochs forms of life differing from those of the present age existed on the earth. It is also generally assumed that all living animals and plants have been derived by gradual modification from previously existing forms. This leads to the further conclusion that those organisms possessing closely similar structure, which are united as species in a genus, are in reality related to one another. It is also probable that the union of corresponding genera into one family and of families into higher groups serves to give expression to a real relationship existing between them.

The presumable origin of a living organism from others previously existing has been distinguished by Haeckel (1) as its phylogenetic development or PHYLOGENY. He termed the series of changes passed through by a living being in attaining its mature condition, its ontogenetic development or ONTOGENY. The supposition, that the successive steps in the ontogenetic development of an organism correspond to those of its phylogenetic development, and that the ontogeny of an organism is accordingly a more or less complete repetition of its phylogeny, was asserted by FRITZ MÜLLER (2), who based his conclusions on the results of comparative research.

The idea of the gradual evolution of higher organisms from lower was familiar to the Greek philosophers, but a scientific basis was first given to this hypothesis in the last century. Through the work of CHARLES DARWIN (3) in particular, who accumulated evidence for a reconsideration of the whole problem of organic evolution, the belief in the immutability of species has been overturned.

DARWIN is the author of the THEORY OF SELECTION. In drawing his conclusions, he proceeded from the variability of living organisms, as shown by the fact that the offspring neither exactly resemble their parents nor each other. Further, he called attention to the constant over-production of offspring, the majority of which must inevitably be destroyed. If this were not so, and all the embryos produced by a single pair attained their full development, they would alone, in a few generations, completely cover the whole surface of the earth. On account of insufficient space for all, the different claimants are engaged in an uninterrupted struggle, in which the victory is gained by those that, for any reason, have an advantage. Through this "struggle for existence" a selective process goes on among the characters appearing in individual variations, and those which under the conditions of life are in any way advantageous tend to be preserved. In this manner DARWIN arrived at the supposition of a process of NATURAL SELECTION, which is the essential of his theory. Newly developed peculiarities arising from individual variability must be inherited in order to become permanent characteristics of a later generation. DARWIN sought in the experience of breeders evidence that such characters are inherited. The breeder selects individuals presenting any desired characters for the purpose of breeding, and has thus formed the races of domesticated animals and cultivated plants. These have often departed so widely from their wild ancestral forms that the latter are not certainly known. Just as in artificial selection, natural selection, although unconsciously, accomplishes this result. As individual peculiarities may be developed by careful breeding and rendered permanent, so by natural selection those qualities which are advantageous in the struggle for existence become more pronounced and are finally confirmed by heredity. By the continued operation of natural selection, organisms must result, which are, in the highest degree, fitted and adapted to their environment. In this way the theory of selection seeks to explain as due to natural causes that adaptability to the environment which is such a striking characteristic of organic life. That the transitional forms in this process of phylogenetic development no longer exist, is accounted for in the theory of natural selection by the assumption that the struggle for existence must necessarily have been most severe between similar organisms. For similar organisms have similar necessities, and the new and better-equipped forms must ultimately prevail over the original less specialised organisms and exterminate them.

Since the publication of Darwin's works many investigators have laboured to advance and make clear our views on phylogeny. Difficulties in applying the results of artificial selection to the natural process became evident, for one main condition of successful artificial selection, the isolation of the organisms from which breeding is taking place, is not fulfilled under natural conditions. Of late years HUGO DE VRIES has endeavoured to obtain an insight into the laws of phylogenetic development by systematic cultivation of particular plants. It would appear from such cultures ([4]) that the starting-point for the origin of new species is not afforded by the "fluctuating variations," which continually occur, but by more marked variations which have been termed "mutations"; these mutations appear suddenly and are strongly inherited. On the other hand it may be said that a sharp line cannot be drawn between mutations and fluctuating variations. DE VRIES tended to assume the existence of a development of the organic world due to original innate capabilities of the living substance, and not dependent on selection. The origin of the large subdivisions of the animal and vegetable kingdoms, the "archetypes," would be due to this sort of evolution ([5]). The organisms have been, and are still, continually influenced by the environment, and by their reaction to external conditions have become more or less directly adapted. In this way striking resemblances in external form have arisen between organisms living under similar conditions although belonging to different archetypes ([6]). Natural selection exercises a constant influence on the process and tends to render species distinct by removing the less advantageous variations.

If the higher organisms have been evolved from the lower, a sharp distinction between plants and animals is excluded. For the characters which are distinctive of animals and plants have appeared in the course of the phylogenetic development of organisms, and were at first wanting. The simplest organisms which now exist are in all probability similar to those which formed the starting-point of this development. The walls which surround the cells composing the plant body, and the green chromatophores within the latter, have been cited as decisive indications of the vegetable character of an organism. Surrounded by firm walls, the living substance becomes more isolated, and, consequently, independence of action in plants, as compared with animals, is diminished. By means of the green colouring matter, plants have the power of producing their own nutritive substances from certain constituents of the air and water, and from the salts contained in the soil, and are thus able to exist independently ; while animals are dependent, directly or indirectly, for their nourishment, and so for their very existence, on plants. Almost all the other differences which distinguish plants from animals may be traced to the structure of plants, or to the manner in which they obtain their food. Another characteristic of plants is the unlimited duration of their ontogenetic development, which is continuous, at the growing points, during their whole life. That none of these criteria are alone sufficient for distinguishing plants from animals is evident from the fact that all the Fungi are devoid of green pigment, and, like animals, are dependent on substances produced by green plants for their nourishment. On the borderland of the two kingdoms, where all other distinctions are wanting, phylogenetic resemblances, according as they may indicate a probable relationship with plants or animals, serve as a guide in determining the position of an organism.

While it is thus impossible to distinguish sharply the two great groups of living organisms from one another, a distinction between them and lifeless bodies is readily recognised. Living organisms are endowed with the quality of IRRITABILITY, in which all lifeless bodies are deficient. External or internal stimuli influence living organisms to an activity, which is manifested in accordance with the requirements and conditions of their internal structure. Even in the smallest known organisms the manifestations of life are occasioned by a similar sensitiveness to external or internal stimuli. It is, therefore, probable that the simplest living beings must have possessed essentially simpler properties than any organisms now known, which would enable us to connect them with non-living substances. The substance which serves as a basis for all development must be supposed to have had an inorganic origin. So far as is actually known, however, all living organisms have arisen only from similar organisms. So far as experience has shown, spontaneous generation is unknown. In the olden times it was a common supposition, which ARISTOTLE himself held, that even highly organised animals and plants could originate from sand and mud. In the same degree that knowledge of the actual development of living organisms was extended, the previously accepted cases of spontaneous generation became more and more restricted, and were finally limited to intestinal worms which could not otherwise, it was thought, be accounted for, and to microscopic organisms, the origin of which also was not understood. Now, for such organisms the possibility of a spontaneous generation has been disproved by more modern investigations; the history of the development of intestinal worms is known, and the germs of minute organisms have been found to exist everywhere. SCHWANN and PASTEUR have been pioneers in this work, and have shown that it is possible to hinder the development of the lower organisms, in places where it is customary to find them, by destroying all existing germs and at the same time preventing the entrance of new ones. It is due to the results obtained by these men in their investigations on spontaneous generation that we are now able to preserve food in a scientific manner. The germs previously existing in the substance to be conserved are destroyed by heat, while, by a proper mode of sealing, the entrance of new germs is rendered impossible, and the decomposition, which their presence would occasion, is accordingly prevented.

All known living organisms have been derived from other living organisms. But the idea of the origin of living from dead substances has on the other hand derived important support from the progress of chemical research. In the early decades of the last century it was customary to draw a distinct line of separation between organic and inorganic chemistry, and to assume that the substances dealt with by organic chemistry could only be produced by the vital action of organisms. The laws governing inorganic chemistry appeared to have no reference to organic chemistry, the formation of organic substance being due to a special force, the "vital force." In 1828 WÖHLER obtained urea from ammonium cyanate, and thus for the first time produced an organic compound from an inorganic substance. In 1845 KOLBE completely synthesised trichloracetic acid, and in 1850 BERTHELOT synthesised alcohol and formic acid. The former substance had been synthetically prepared by HENNEL in 1828, but BERTHELOT was the first to recognise its identity with the substance formed in alcoholic fermentation. By these results the former distinction between organic and inorganic chemistry was destroyed. Organic chemistry has become the chemistry of carbon compounds.

In some such way it is possible that living matter originated from non-living at some period in the evolution of the earth when the conditions for its formation existed. In order that the organic world should have developed from the first living matter, one of the original properties of the latter must have been a capability of continued existence among its surroundings. It must have been capable of variation and of retaining the new characters appearing in this way, of growth, *i.e.* the increase of itself at the cost of foreign substances, and of reproduction, *i.e.* multiplication by separation into a number of parts. Some observers have recently described the origin of microscopic structures which behave similarly to living beings in bouillon and other organic culture media when exposed to the action of radium [7].

Botany, or the science of plants, may be divided into a general and a special part. In the general part, the structure and functions of plants as such will be considered; in the special part, the particular structure and functions of the separate orders of plants will be discussed.

The study of the structure of plants is called MORPHOLOGY; that of their functions PHYSIOLOGY. In the general part, morphology and physiology will be treated separately; in the special part, conjointly.

MARINE BIOLOGICAL LABORATORY
WOODS HOLE
LIBRARY
MASS.

PART I

GENERAL BOTANY

SECTION I

MORPHOLOGY

MARINE BIOLOGICAL LABORATORY
LIBRARY
WOODS HOLL, MASS.

GENERAL BOTANY

SECTION I

MORPHOLOGY

THE object of vegetable morphology is the scientific study of the forms of plants. It does not attempt to discover the causes of the variation in the forms, but rather has accomplished its purpose when it succeeds in showing how one form may be derived from another. The only real basis of morphological study is, accordingly, the genealogical development or phylogeny (p. 2). As phylogenetic development can only be inferred, and cannot be directly followed, the methods of morphology must also be indirect. They are dependent on the one hand upon ontogeny, *i.e.* on the study of the development passed through by an organism in attaining its mature condition, and on the other hand upon the comparison of existing organisms with one another and with those that have become extinct. To a certain extent the ontogenetic development of a plant repeats its phylogeny and helps to elucidate the latter, while, by means of comparative investigation, extreme forms may be connected by intermediate links. As, however, the ontogeny of a plant is neither a complete nor invariable repetition of its phylogeny, and as connecting links between extreme forms are often wanting, the results of morphological study are frequently incomplete. Such parts or members of plants which it is reasonable to presume have had a common origin are distinguished as HOMOLOGOUS; those which, while probably having different origins, yet exercise the same functions, are termed ANALOGOUS. Through the adaptation of different parts to the same function, a similarity in both external form and internal structure often results; and in this way the correct determination of morphological relationships is rendered difficult. Only homologous parts have the same "morphological value." This homology is determined by the facts of phylogeny and origin, and not by any correspondence in function. Though the function of any structure does not influence its morphological value, the need of making clear the intimate connection between form and function often introduces physiological considerations into morphological questions. When, for phylogenetic reasons, it seems possible to attribute to a number of different members a common origin, such a hypothetical original form is termed the fundamental or primitive form. The various modifications which the primitive form has passed through constitute its METAMORPHOSIS. In this way the theory of the metamorphosis of plants, which was once but an ideal conception, acquires an actual significance.

Slightly differentiated structures, which are found at the beginning of a series of progressively differentiating forms, are termed RUDIMENTARY; imperfect structures, which have arisen as the result of the deterioration of more perfect forms, are termed REDUCED.

Vegetable morphology includes the study of the external form and the internal structure of plants. The descriptive study of the external form of plants has been termed organography (8). This term will not be used, since by the use of the word "organ," it would seem to have a physiological signification. Morphology takes no recognition of the parts of a plant as organs, but treats of them merely as members of the plant body. On the other hand, one of the most important aims of physiology is to place the external form and the internal structure of the living body in relation to the functions performed by the latter; physiology also investigates the causes of the organisation. The study of the internal structure of plants is often designated Anatomy or Phytotomy; but as it usually includes also the study of the more minute internal structure, it resembles rather histology, in the sense in which that term is used by zoologists, and concerns itself to a much less degree with the coarse anatomy of the plant body. In any case, it is the simplest plan to designate the study of the outer form EXTERNAL MORPHOLOGY, and that of the inner structure INTERNAL MORPHOLOGY.

I. EXTERNAL MORPHOLOGY (9)

Plants show a great diversity in the form and arrangement of their members; it is the task of morphology to determine the points of agreement existing between them. It seeks to do this by determining the common origin of the homologous parts or members.

The Development of Form in the Plant Kingdom

The Thallus (^{10}).—When the body of a plant is not differentiated into separate members, or is composed of members which (though they may be similar) are not homologous with those of the most highly organised plants, it is termed a THALLUS. When the thallus is differentiated into members analogous to those of the higher plants some confusion may arise from the same names being used for parts which, since their origin has been distinct, are not homologous.

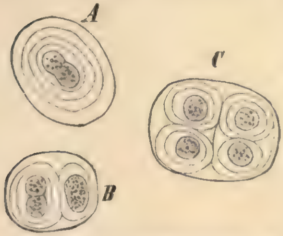


FIG. 1.—*Gloeocapsa polydermatica.* *A*, Commencement of division; *B*, (to the left) shortly after division; *C*, a resting stage. (× 540.)

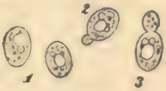


FIG. 2.—*Saccharomyces cerevisiae.* 1, Cells without buds; 2 and 3, budding cells. (× 540.)

The simplest form that we can imagine for an organism is that of a sphere, and this is actually the form of some of the lower plants. A green growth often seen on damp walls consists of an aggregation of the microscopically small spherical bodies of *Gloeocapsa polydermatica* (Fig. 1), an Alga belonging to one of

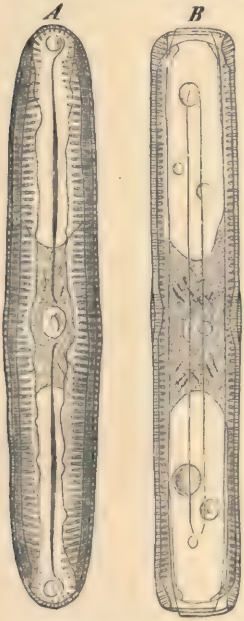


FIG. 3.—*Pinnularia viridis.* *A*, Surface view; *B*, lateral view. (× 540.)

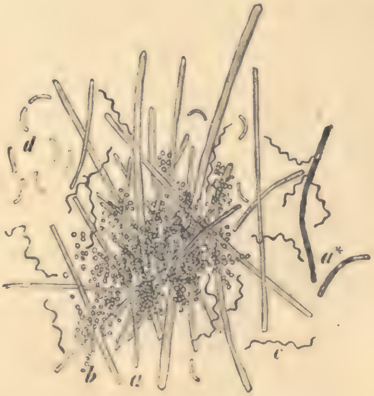


FIG. 4.—Bacteria from deposits on teeth. *a*, *Leptothrix buccalis*; a^*, the same after treatment with iodine; *b*, *Micrococcus*; *c*, *Spirochaete dentium* after treatment with iodine; *d*, *Spirillum sputigenum*. (× 800.)

the lowest divisions of the vegetable kingdom. The single plants of the Beer-yeast (*Saccharomyces cerevisiae*) are ellipsoidal; but, from their peculiar manner of growth, by budding, they form lateral outgrowths, and thus often appear constricted (Fig. 2). Cylindrical and also disc-shaped forms are shown by various Algae. The Diatomeae (Fig. 3), in particular, exhibit a great variety of spindle, canoe, helmet, and fan-like shapes; but they may all be derived from the more simple spherical, discoidal, or cylindrical forms.

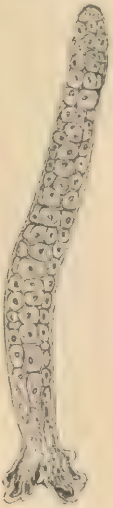


Fig. 5.—*Ulva Lactuca*, young stage, showing apex and base. × 220.)

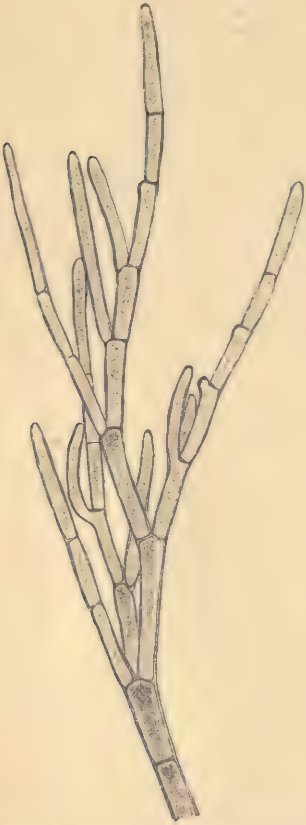


Fig. 6.—Portion of *Cladophora glomerata*. (× 48.)

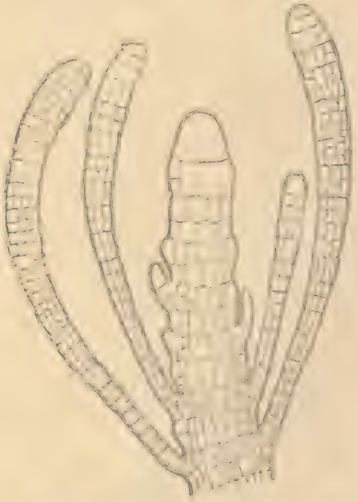


Fig. 7.—*Cladostephus verticillatus*. (After Pringsheim, × 30.)

Among the Bacteria, which, as the cause of infectious diseases and of decomposition, have been the object of so much recent investigation, we also meet with spherical, rod-shaped, filamentous, and spirally wound forms (Fig. 4). The next stage in the progressive development of external form in the vegetable kingdom is exhibited by such plants as show a DIFFERENTIATION INTO APEX AND BASE. The base serves as a point of attachment, while growth is localised at the apex. In this way a growing point is developed at the apex. As an example of such a form, a young plant of the green Alga, *Ulva Lactuca* (Fig. 5), may be taken. The development of a more complicated external form is represented by the branched filamentous, or ribbon-shaped Algae, in which the origin of new formations is more and more restricted to the apex. An ACROPETAL order of development, in which the youngest lateral members are always nearest the growing apex, is clearly demonstrated by the branched filaments of the common green Alga, *Cladophora glomerata* (Fig. 6). Still more pronounced is the apical growth in the brown seaweed *Cladostephus verticillatus* (Fig. 7). The great variety in the form of the larger Fungi and Lichens, by which they are distinguished as club-, umbrella-, salver-, or bowl-shaped, or as bearded or shrub-like, comes about by the union or intertwining of apically growing filaments. This type of construction is limited to Fungi and Lichens. As the apex itself may undergo successive bifurcation, as in the case of *Dictyota dichotoma* (Fig. 8), it does not always necessarily follow that new members must be formed beneath the original apex.

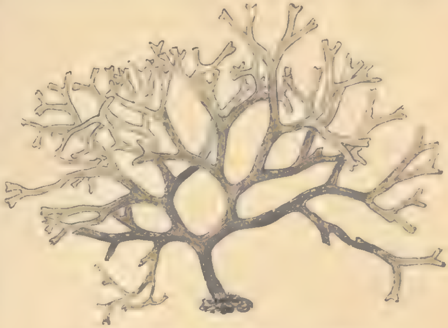


FIG. 8.—*Dictyota dichotoma*. ($\frac{2}{3}$ nat. size.)

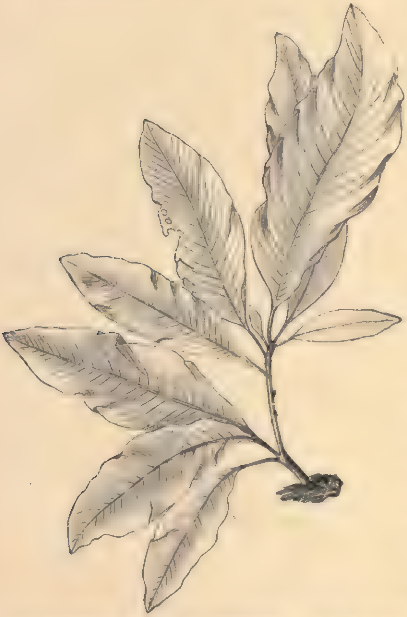


FIG. 9.—*Hydrolapathum sanguineum*. ($\frac{1}{2}$ nat. size.)

The highest degree of external differentiation among the lower plants is met with in certain groups of red and brown sea-weeds (Rhodophyceae and Phaeophyceae). Many representatives of these classes resemble the higher plants in the formation and arrangement of their members; *Hydrolapathum sanguineum* (Fig. 9), for example, as is indicated by its name, resembles a species of *Rumex*, and affords an instructive illustration of the analogy of form existing between plants phylogenetically widely distinct from one another. The progressive differentiation of the thallus of the Bryophyta (Mosses and Liverworts) presents an even closer parallel to the organisation of the higher plants. Within the group of the Liverworts (*Hepaticae*) are found ribbon-shaped forms and others that show a division into distinct members. Thus the thallus of *Riccia fluitans* (Fig. 10) is ribbon-shaped and dichotomously branched, and its habit or general appearance recalls the Brown Alga *Dictyota dichotoma* mentioned above (Fig. 8). *Blasia pusilla* (Fig. 11) has marginal indentations in its ribbon-shaped body. Lastly, *Plagiochila asplenioides* (Fig. 12), another Liverwort, has a distinction of stem-like and leaf-like members which is completely analogous to that exhibited by the most highly organised plants. In spite of this variety in external form, and the high organisation that may be reached, the body of these lower plants is termed a thallus, and they are grouped together as Thallophytes in contrast to the higher plants or Cormophytes.

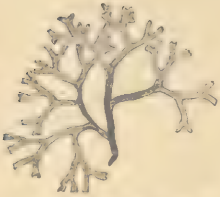


FIG. 10.—*Riccia fluitans.* (Nat. size.)

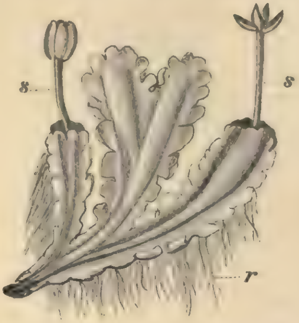


FIG. 11.—*Blasia pusilla.* *s*, Sporogonium; *r*, rhizoids. (× 2.)

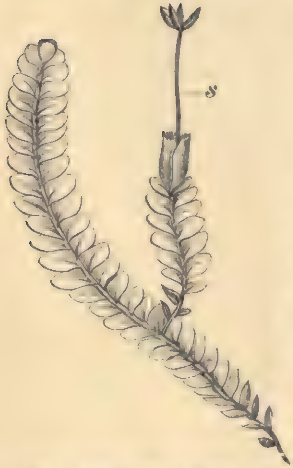


FIG. 12.—*Plagiochila asplenioides.* *s*, Sporogonium. (Nat. size.)

The Cormus.—All plants, from the Pteridophtya or fern-like plants onwards, may be grouped together as CORMOPHYTES. It may be assumed that they have had a common origin, and that the similarity of their organisation is due to true homology. In addition to the distinction of stem and leaf in their shoots, they possess true roots, while even the most highly organised Bryophyta have only filamentous structures (rhizoids) (Fig. 11 *r*) in place of roots to attach them to the substratum. True roots, on the other hand, which appear for the first time in the Pteridophyta, are, for the most part, cylindrical structures with apical growth. Besides possessing a distinctive internal construction they are distinguished in their external form from the shoot by having a special sheath, the ROOT-CAP or CALYPTRA covering the growing point, and by the absence of leaves. The body of the higher plants provided with stem, root, and leaf is termed a cormus, and the plants are spoken of as cormophytes.

The Metamorphosis of the Primary Members of Cormophytes.—After the differentiation into stem and leaf and the appearance of the roots had taken place, further changes have consisted essentially in a more or less profound modification of these primary members of the cormophytic plant-body. Such changes are spoken of as a metamorphosis (p. 10), and in some cases may be so extensive as to lead to one primary member assuming the characters of another.

The relationships between homologous members, which are often very striking, did not escape the notice of earlier observers. They suggested comparisons, although no real phylogenetic basis for such comparisons existed. Thus, an idealistic conception of the form of external members was developed, and finally reached its highest artificial development in GOETHE's Theory of Metamorphosis ; and its scientific conclusion in the writings of ALEXANDER BRAUN. As the great variety exhibited in the external appearance of the lower plants precluded any possibility of assigning to them hypothetical primitive forms, the whole terminology of the external morphology of plants has been derived from conceptions applicable only to the Cormophytes. Even to-day, the same terms used in reference to the Cormophytes are applied to parts of the Thallophytes, which are evidently only analogous.

Members of Independent Origin.—Parts which cannot be derived by metamorphosis of the primary members of the cormophytic plant are sometimes met with. Though they are of infrequent occurrence they are of importance as showing that the natural evolutionary process is not to be limited by any formal scheme. Such structures will be discussed farther on.

Relations of Symmetry

Every section through a part of a plant, made in the direction of its longitudinal axis, is distinguished as a longitudinal section ; those at right angles to it being termed cross or transverse sections. Parts of plants which may be divided by a number of longitudinal planes into like halves are termed either MULTILATERAL, RADIAL, or ACTINOMORPHIC. Such parts are symmetrically constructed around their longitudinal axis. The degree of symmetry peculiar to any leafy shoot will be more apparent from a diagram, that is if the leaves which it bears be projected on a plane at right angles to its axis. The radial symmetry of a shoot with opposite leaves is clearly shown in the adjoining diagram (Fig. 13). A shoot with its leaves arranged alternately in two rows shows somewhat different relations of symmetry. The diagram of such a shoot (Fig. 14) can only be divided into similar halves by two planes. When such a condition exists, a member or plant is said to be BILATERAL. When, however, a division into two similar halves is only possible in one plane, the degree of symmetry is indicated by the terms DORSIVENTRAL or ZYGOMORPHIC; since, while the right and left halves correspond to one another, differences exist between the dorsal and ventral surfaces. Ordinary foliage-leaves exhibit this dorsiventral structure. In the accompanying figure (Fig. 15) such a monosymmetrical, dorsiventral foliage-leaf is diagrammatically represented. From the surface view (*A*) and from the cross-section (*B*), in which the distinction between the dorsal and ventral sides is indicated by shading, it is obvious that but one plane of symmetry (*s*) can be drawn. Dorsiventral members are often ASYMMETRICAL, not being divided by any plane into corresponding halves: the leaves of many kinds of *Begonia* will

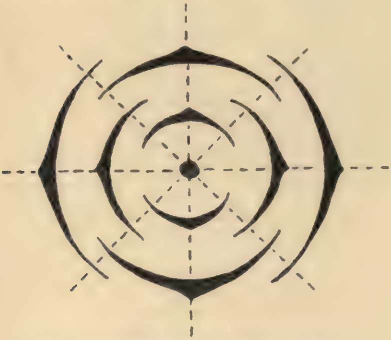


FIG. 13.—Diagram showing the so-called decussate arrangement of leaves.

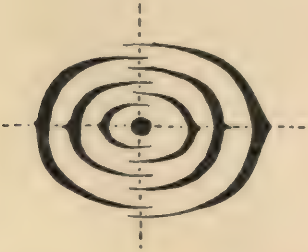


FIG. 14.—Diagram showing two-ranked alternate arrangement of leaves.

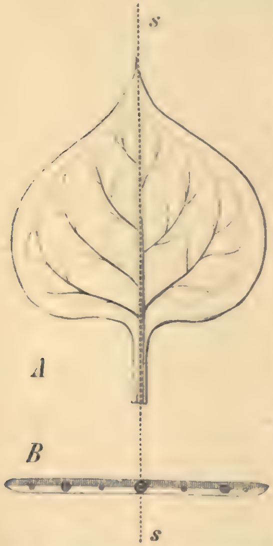


FIG. 15.—Diagram of a foliage-leaf. *A*, Surface view; *B*, transverse section; *s*, plane of symmetry.

serve as examples of this. In such cases—and the leaf of the Elm may be mentioned as another striking example—the symmetry of the individual leaf is subordinated to that of the entire plant.

Branch Systems

Thallophytes as well as Cormophytes exhibit systems of branching, resulting either from the formation of new growing points by the bifurcation of a previously existing growing point, or from the development of new growing points in addition to those already present. In this way there arise two systems of branching, the DICHOTOMOUS and the MONOPODIAL. By the uniform development of a continuously bifurcating stem, a typical dichotomous system of branching is produced, such as is shown in *Dictyota dichotoma* (Fig. 8), and is represented diagrammatically in Fig. 16 *Aa*. In a typically developed example of the monopodial system there may always be distinguished a persisting main axis, the MONOPODIUM, giving rise to lateral branches from which, in turn, other lateral branches are developed. A good example of this form of branching is afforded by a Fir-tree. Where one of the two branches is regularly developed at the expense of the other, the dichotomous system assumes an

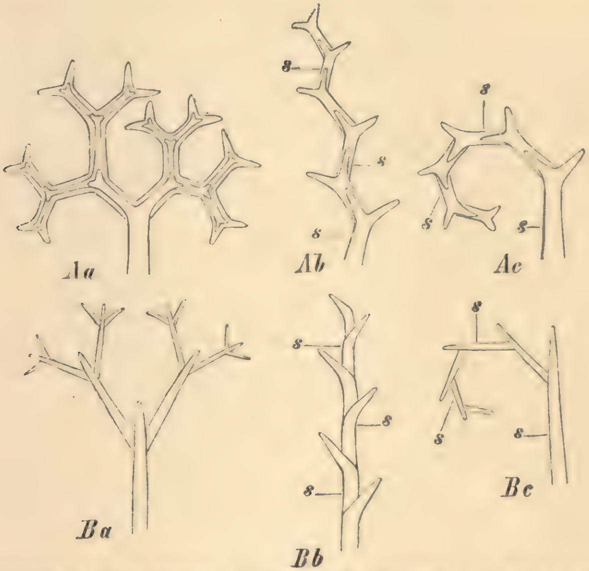


FIG. 16.—Diagrams of branch systems. *A*, Dichotomous branching; *Aa*, equal dichotomy; *Ab*, scorpioid dichotomy; *Ac*, helicoid dichotomy. *B*, monopodial branching; *Ba* false dichotomy; *Bb*, scorpioid cyme; *Bc*, helicoid cyme; *s*, *s*, sympodia.

appearance quite different from its typical form. The more vigorous branches may then, apparently, form a main axis, from which the weaker branches seem to spring, just as if they were lateral branches. This mode of branching (Fig. 16 *Ab*) is illustrated by the Selaginellas. Such an apparent main axis (*s*, *s*) is termed, in accordance with its origin, a SYMPODIUM. On the other hand, in the monopodial system two or even several lateral branches may develop more strongly than the main axis, and so simulate true DICHOTOMY or POLYTOMY. Such monopodial forms of branching are referred to as FALSE DICHOTOMY (Fig. 16 *Ba*) or FALSE POLYTOMY, as the case may be. A good example of false dichotomy may be seen in the Mistletoe (*Viscum album*). If, however, a lateral branch so exceeds the main axis in development pushing the apex of the latter to one side, that it seems ultimately to become a prolongation of the axis itself, a sympodium is again formed (Fig. 16 *Bb*). This is what occurs in many of our forest trees, *e.g.* the Lime and Beech; in both of these trees the terminal buds of each year's growth die, and the prolongation of the stem, in the following spring, is continued by a strong lateral bud, so that in a short time its sympodial origin is no longer recognisable. In many rhizomes, on the other hand, the sympodial nature of the axis can be easily distinguished; as, for example, in the rhizome of *Polygonatum multiflorum* (Fig. 23), in which, every year, the terminal bud gives rise to an aerial shoot, while an axillary bud provides for the continuance of the axis of the rhizome. In the flower-producing shoots or inflorescences of Phanerogams the different systems of branching assume very numerous forms. These will be more fully described in their proper place. To such inflorescences belong the ventrally coiled dorsiventral shoots which produce new shoots from their convex dorsal surfaces, instead of in their leaf-axils.

The Shoot

The Development of the Shoot.—Under the term shoot a stem and its leaves are collectively included. A stem possesses an apical mode of growth (Fig. 17), and its unprotected growing point is described as naked, in contrast to that of the root with its sheathing root-cap. The apex of the shoot generally terminates in a conical protuberance, called the VEGETATIVE CONE. As it is usually too small to be clearly visible to the unaided eye, it is best seen in magnified median longitudinal sections. So long as the apex of the shoot is still internally undifferentiated, it continues in the embryonic condition, and it is from the still embryonal vegetative cone that the leaves take their origin. They first appear in acropetal succession as small, conical protuberances, and attain a larger size the farther removed they are from the apex of the stem. As the leaves usually grow more rapidly than the stem which produces them, they envelop the more rudimentary leaves, and, overarching the vegetative cone, form a BUD. Buds are therefore merely undeveloped shoots. If they are to remain for a long time undeveloped, as for example is the case with winter buds, they are protected in a special manner during their period of rest.

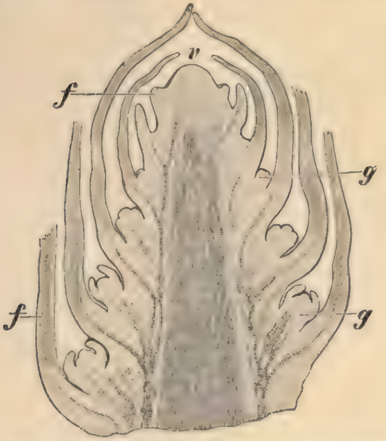


FIG. 17.—Apex of a shoot of a phanerogamic plant. *v*, Vegetative cone; *f*, leaf rudiment; *g*, rudiment of an axillary bud. (× 10.)

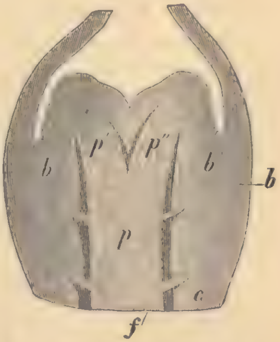


FIG. 18.—Longitudinal section of a bifurcating shoot (*p*) of *Lycopodium alpinum*, showing equal development of the rudimentary shoots, *p*′, *p*″; *b*, leaf rudiments; *c*, cortex; *f*, vascular strands. (After HEGELMAIER, × 60.)

The Origin of New Shoots.—The formation of new growing points by the bifurcation of an older growing point, in a manner similar to that already described for *Dictyota dichotoma* (Fig. 8), occurs also in the lower thalloid Hepaticae (*Riccia fluitans*, Fig. 10). Among the Cormophytes this method of producing new shoots is of less frequent occurrence, and is then mainly limited to the Pteridophytes, and is typically shown only in some Lycopodiaceae. In this case, whenever a shoot is in process of bifurcation, two new vegetative cones are formed by the division of the growing point (Fig. 18). In most of the Lycopodiaceae the new shoots thus formed develop unequally; the weaker becomes pushed to one side and ultimately appears as a lateral branch (Fig. 19). Although a relationship as regards position is generally apparent between the origin of leaves and the lateral shoots, in the system of branching resulting from such a bifurcation of the vegetative cone this connection does not exist. In the more highly developed Bryophytes, particularly in the true Mosses, new shoots arise obliquely below the still rudimentary leaves

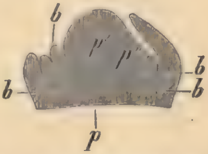


FIG. 19.—Bifurcating shoot (*p*) of *Lycopodium inundatum*, showing unequal development of the rudimentary shoots, *p*′, *p*″; *b*, leaf rudiments. (After HEGELMAIER, × 40.)

at some distance from the growing point. In the Phanerogams new shoots generally arise in the axils of the leaves. In the accompanying illustration of a longitudinal section of a phanerogamic shoot (Fig. 17) the rudiment of a shoot (*g*) is just appearing in the axil of the third uppermost leaf; in the axils of the next older leaves the conical protuberances of the embryonic leaves are already beginning to appear on the still rudimentary shoot. Shoots thus produced in the axils of leaves are termed AXILLARY SHOOTS. The leaf, in the axil of which a shoot develops, is called its SUBTENDING LEAF. An axillary shoot is usually situated in a line with the middle of its subtending leaf, although it sometimes becomes pushed to one side. As a rule, only one shoot develops in the axil of a leaf, yet there are instances where it is followed by additional or ACCESSORY SHOOTS, which either stand over one another (serial buds), as in *Lonicera*, *Gleditschia*, *Gymnocladus*, or side by side (collateral buds), as in many Liliaceae, *e.g.* species of *Allium* and *Muscari*.

Although in the vegetative regions, *i.e.* the regions in which merely vegetative organs are produced, the rudiments of the new shoots of phanerogamic plants make their appearance much later than those of the leaves, in the generative or flower-producing regions the formation of the shoots follows directly upon that of their subtending leaves, or the shoots may even precede the leaves. In this last case the subtending leaves are usually either poorly developed or completely suppressed, as in the inflorescence of the Cruciferae.

The bud forming the end of a shoot is called the terminal bud, while those borne on the sides of the shoot are the lateral buds.

Shoots developing in predetermined positions on young parts of the plant are designated NORMAL, in contrast to ADVENTITIOUS SHOOTS, which are produced irregularly from the old or young portions of a plant. Such adventitious shoots frequently spring from old stems, also from the roots of herbaceous plants (*Brassica oleracea*, *Anemone sylvestris*, *Convolvulus arvensis*, *Rumex Acetosella*), or of bushes (*Rubus*, *Rosa*, *Corylus*), or of trees (*Populus*, *Ulmus*, *Robinia*). They may even develop from leaves, as in *Cardamine pratensis*, *Nasturtium officinale*, and a number of Ferns. An injury to a plant will frequently induce the formation of adventitious shoots, and they frequently arise from the cut surface of stumps of trees. Gardeners often make use of pieces of stems, rhizomes, or even leaves as cuttings from which to produce new plants.

Leaves and also normal shoots, which make their appearance as outgrowths from the portions of the parent shoot, still in an embryonic condition, have an external or EXOGENOUS origin. Adventitious shoots, on the other hand, which arise from the older parts of stems or roots, are almost always ENDOGENOUS. They must penetrate the outer portions of their parent shoot before becoming visible. Adventitious shoots formed on leaves, however, arise, like normal shoots, exogenously.

Buds are formed in the marginal indentations of the fleshy leaves of species of *Bryophyllum* (Crassulaceae). Although arising from the leaf these buds must properly be regarded as "normal," and as forming part of the normal ontogeny of the plant, since they arise in pre-determined positions from young tissue. In the strict sense of the term only those buds can be called adventitious which are produced in casual positions from tissues which in their production enter into renewed activity, *e.g.* the buds which arise at the base of isolated leaves of *Begonia* when these are laid on damp soil. The concept of "normal buds" is notwithstanding usually taken in a narrower sense and limited to buds which arise on the axis of the shoot in the normal course of development. Examples, however, occur which make it difficult to draw a sharp distinction in this latter sense between normal and adventitious shoot-formation ([11]).

While, as a rule, new leaves arise beneath the apex of a stem, which continues to grow, exceptions to this occur, especially in floral structures; the apical cone may be used up in the formation of a terminal leaf-rudiment. In this way many of the stamens and carpels of Phanerogams, which are described as terminal, arise.

In some shoots of limited growth such as the inflorescences of many Phanerogams (*Vallisneria*) new lateral members arise in an inverted order proceeding from the apex towards the base. The introduction of new lateral members between those already present is also met with in the floral region ([12]).

It was mentioned above that normal shoots arose from the embryonic tissue of the growing point of the parent shoot. When they are apparent at a greater distance from the apex (Fig. 17) it can usually be shown that embryonic substance has been reserved at the proper points for their formation. The growing points of adventitious shoots are for the most part derived from embryonic tissues which have persisted in the older portions of the plant and are capable of increase. They can, however, also arise from older tissues, owing to the capability of the latter to return to the embryonic condition and produce new growing points.

Further Development of the Shoot.—The processes of development, which result in the production of new members at the apex of a shoot, are followed by their increase in size and further growth. This growth is usually introduced by the vigorous elongation of the segments, which is spoken of as growth in length, while at the same time the buds expand. The zone of most rapid growth in length is at some distance from the growing point. The growth in length and consequent elongation of the shoot is in some cases so slight that the leaves remain close together, and leave no free spaces on the stem, thus forming so-called SHORT SHOOTS. The same plant may bear ordinary elongated shoots and short shoots. The duration of life of the latter is usually shorter, and they frequently do not branch, and take no part in the permanent branch system of the tree. This is seen in the Larch, in which the short shoots with crowded needle-shaped leaves are borne on elongated shoots. The stem of a shoot, as contrasted with the leaves, is often spoken of as the AXIS; the portions of the stem axis between the insertions of the leaves are termed the INTERNODES, and the parts of the axis, from which the leaves arise, the NODES. When the base of the leaf encircles the stem, or when several leaves take their origin at the same node, the nodes often become strongly marked (Labiatae).

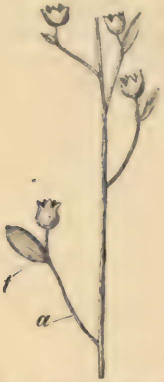


FIG. 20.—*Samolus Valerandi*, each axillary shoot (*a*) bearing its subtending leaf (*t*), and terminating in a fruit. (Nat. size.)

In some cases the growth in length of a shoot continues for a longer time at certain intermediate points by means of INTERCALARY GROWTH. Such regions of intercalary growth are generally situated at the base of the internodes, as in the case of the Grasses. A displacement from the position originally occupied by the members of a shoot frequently results from intercalary growth. A bud may thus, for example, become pushed out of the axil of its subtending leaf, and so apparently have its origin higher on the stem; or a subtending leaf, in the course of its growth, may carry its axillary bud along with it, so that the shoot which afterwards develops seems to spring directly from its subtending leaf; or, finally, the subtending leaf may become attached to its axillary shoot, and growing out with it, may thus appear to spring from it (Fig. 20).

In the annual growth in length of a shoot of a tree, *i.e.* the increment formed during one vegetative period, the lowest internodes which intervene between the bud-scales are very short. By means of the closely crowded scars of the bud-scales the limits of the shoots formed in successive years can be determined.

Resting Buds.—As a means of protection against loss of water in our latitudes, the buds of shrubs and trees are usually invested, in winter, with scale-like leaves or BUD-SCALES (Fig. 21). These are rendered still more effective as protective structures by hairy outgrowths and excretions of resin and gum, and also by the occurrence of spaces filled with air between the scales. Not infrequently the subtending leaf takes part in the protection of its axillary bud, the base of the leaf-stalk, after the leaf itself has fallen, remaining on the shoot as a cap-like covering for the winter bud. The buds of tropical plants, which have to withstand a dry period, are similarly protected; but

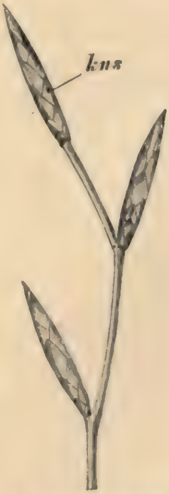


FIG. 21.—Winter buds of the Beech (*Fagus silvatica*). *kns*, Bud-scales. (Nat. size.)

where the rainfall is evenly distributed throughout the year buds develop no such means of protection.

In many deciduous trees, such as the Willow, the terminal buds of the year's growth regularly die. In nearly all trees many buds, usually the first-formed buds of each year's shoot, seem able to remain dormant during many years without losing their vitality: these are termed DORMANT BUDS. In the case of the Oak or Beech such latent buds can endure for hundreds of years; in the meantime, by the elongation of their connection with the stem, they continue on its surface. Often it is these, rather than adventitious buds, which give rise to the new growths formed on older parts of stems. It may sometimes happen that the latent buds lose their connection with the woody parts of their parent stem, but nevertheless grow in thickness, and develop their own wood; they then form remarkable spherical growths within the bark, which may attain the size of a hen's egg and can be easily separated from the surrounding bark. Such globular shoots are frequently found in Beech and Olive trees.

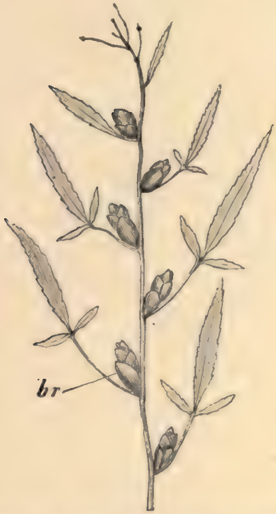


FIG. 22.—Shoot of *Dentaria bulbifera*, bearing bulbils, *br*. (Nat. size.)

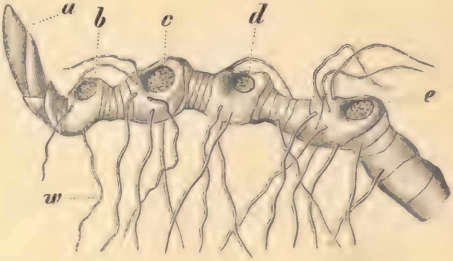


FIG. 23.—Rhizome of *Polygonatum multiflorum*. *a*, Bud of next year's aerial shoot; *b*, scar of this year's, and *c*, *d*, *e*, scars of three preceding years' aerial shoots; *w*, roots. (¾ nat. size.)

The Metamorphosis of the Bud.—The BULBILS and GEMMÆ, which become separated from the parent plant and serve as a means of reproduction, are special forms of modified buds. To facilitate the storage of reserve nutritive substances they have usually the form of small tuberous bodies. Many plants owe their specific name to the fact that they produce such bulbils, as, for example, *Lilium bulbiferum* and *Dentaria bulbifera* (Fig. 22).

The Metamorphosis of Subterranean Shoots.—Shoots that live underground undergo characteristic modifications, and are then termed

ROOT-STOCKS OF RHIZOMES. By means of such subterranean shoots many herbaceous perennial plants are enabled to persist through the winter. A rhizome develops only reduced leaves in the form of larger or smaller, sometimes scarcely visible, scales. By the presence of such scale leaves, with their axillary buds, and by the absence of a root-cap, as well as by its internal structure, a rhizome may be distinguished from a root. Rhizomes usually produce numerous roots; but in a few cases these are wanting and the rhizome itself functions as a root. Rhizomes often attain a considerable thickness and store up nutritive material for the formation of aerial shoots. In the illustration on the preceding page (Fig. 23) is shown the root-stock of Solomon's Seal (*Polygonatum multiflorum*). At *d* and *c* are seen the scars of the aerial shoots of the two preceding years; and at *b* may be seen the base of the stem growing at the time the rhizome was taken from the ground, while at *a* is shown the bud of the next year's aerial growth. The rhizome of *Coralliorrhiza innata*, a saprophytic Orchid, which grows in soil rich in humus, affords a good example of a root-stock functioning as a root (Fig. 24). BULBS, also, belong to the class of metamorphosed shoots. They represent a shortened shoot with a flattened, discoid stem (Fig. 25 *zk*), the fleshy

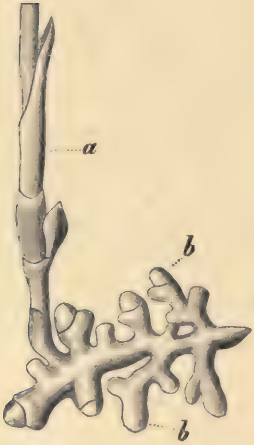


FIG. 24.—Rhizome of *Coralliorrhiza innata*. *a*, Floral shoot; *b*, rudiments of new rhizome branches. (After SHACHT, nat. size.)

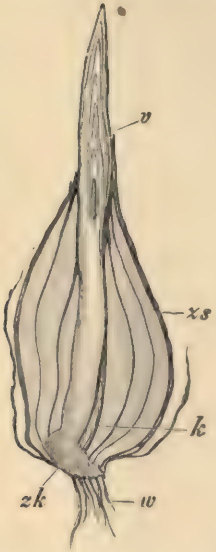


FIG. 25.—Longitudinal section of Tulip bulb, *Tulipa Gesneriana*. *zk*, Modified stem; *zs*, scale leaves; *v*, terminal bud; *k*, rudiment of a young bulb; *w*, roots. (Nat. size.)

thickened scale leaves (*zs*) of which are filled with reserve food material. The aerial growth of a bulb develops from its axis, while new bulbs are formed from buds (*k*) in the axils of the scale leaves. Another form of underground shoot, allied to bulbs and connected with them by transitional forms, is distinguished as a TUBER. The axis of a typical tuber, in contrast to that of a bulb, is fleshy and swollen, serving as a reservoir of reserve material, while the leaves are thin and scaly. Of such tubers those of the Meadow Saffron (*Colchicum autumnale*) or of *Crocus sativus* are good examples. In the Meadow Saffron new tubers arise from axillary buds near the base of the modified shoot, but in the Crocus from buds near the apex. In consequence of this, in the one case the new tubers appear to grow out of the side, and in the other to spring from the top of the old tubers. The tubers of the Potato (Fig. 26) or of the Jerusalem Artichoke (*Helianthus tuberosus*) are also subterranean shoots with swollen axis and reduced leaves. They are formed from the ends of branched, underground shoots or runners (STOLONS) and thus develop at a little distance from the parent plant. The so-called eyes on the outside of a potato, from which the next year's growth arises, are in reality axillary buds, but the scales which represent their subtending leaves can only be distinguished on very young tubers. The parent plant dies after the formation of the tubers, and the reserve food stored in the tubers nourishes the shoots which afterwards develop from the eyes. Since, in their uncultivated state, the tubers of the Potato plant remain in the ground and give rise to a large number of new plants, it is of great advantage to the new generation that the tubers are produced at the ends of runners, and are thus separated from one another.

The Metamorphosis of Aerial Shoots.—Similar advantages to those obtained by the elongation of the underground shoots in the Potato accrue from surface runners, such as are produced on Strawberry plants. Surface runners also bear scale-like leaves with axillary buds, while roots are developed from the nodes. The new plantlets, which arise from the axillary buds, ultimately form independent plants by the death of the intervening portions of the runners.

Still more marked is the modification exhibited by shoots which only develop reduced leaves, while the stems become flat and leaf-like and assume the functions of leaves. Such leaf-like shoots are called CLADODES or PHYLLOCLADES, and Goebel proposes to distinguish those flattened shoots which have limited growth and specially leaf-like appearance as phylloclades, and to term other flattened axes cladodes. Instructive examples of such formations are furnished by *Ruscus aculeatus* (Fig. 27), a small shrub whose stems bear in the axils of their scale-like leaves (*f*) broad, sharp-pointed cladodes (*cl*), which have altogether the appearance of leaves. The flowers arise from the upper surface of these cladodes, in the axils of scale leaves.

In like manner the stems of the Opuntias (Fig. 28) are considerably flattened, while the leaves are reduced to small thorny protuberances.

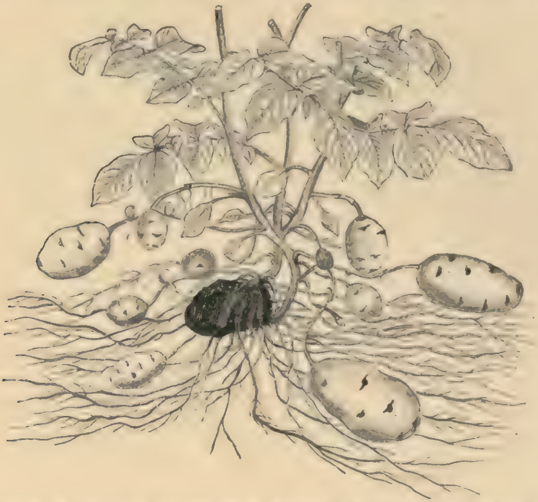


FIG. 26.—Part of a growing Potato plant, *Solanum tuberosum*. The whole plant has been developed from the dark-coloured tuber in the centre. (From nature, copied from one of BAILLON's illustrations, ⅓ nat. size.)

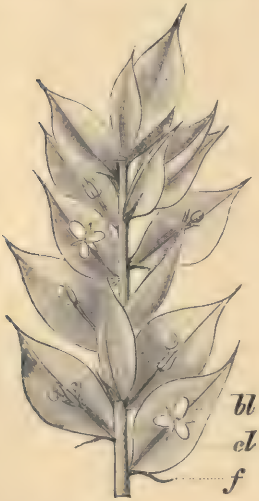


FIG. 27.—Twig of *Ruscus aculeatus*. *f*, Leaf; *cl*, cladode; *bl*, flower. (Nat. size.)

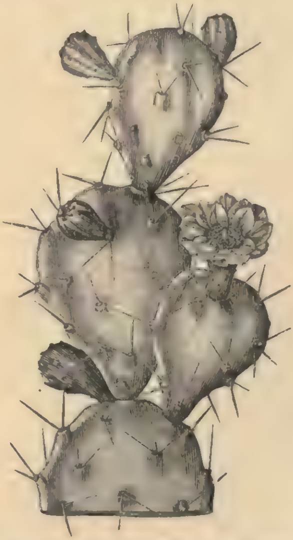


FIG. 28.—*Opuntia monacantha*, Haw., showing flower and fruit. (After SCHUMANN, ⅕ nat. size.)

In this case the juicy flat shoots perform not only the functions of assimilatory organs, but also serve as water-reservoirs in time of drought.

On the other hand a plant may lose its leaves more or less completely without any marked flattening or thickening occurring in the stems, which then take on a green colour; this, for example, is the case in the Broom (*Spartium scoparium*), which develops only a few quickly falling leaves on its long, naked twigs. As a rule, however, leafless green Phanerogams will be found to have swollen stems, as in the variously shaped species of *Euphorbia* and *Cactus*.

Reduction of the Shoot in Parasites.—A great reduction in the leaves, and also in the stems, often occurs in phanerogamic parasites, in consequence of their parasitic mode of life. The leaves of the Dodder (*Cuscuta*, Fig. 202 *b*) are only represented by very small yellowish scales, and the stem is similarly yellow instead of green. The green colour would, in fact, be superfluous, as the Dodder does not produce its own nourishment, but derives it from its host plant. *Cuscuta Trifolii*, one of the most frequent of these parasites, is often the cause of the large yellow areas frequently observable in the midst of clover fields. In certain tropical parasites belonging to the family Rafflesiaceae, the process of reduction has advanced so far that the flowers alone are left to represent the whole plant. *Rafflesia Arnoldi*, a plant growing in Sumatra, is a remarkable example of this; its flowers, although they are a metre wide, the largest flowers in existence, spring directly from the roots of another plant (species of *Cissus*).

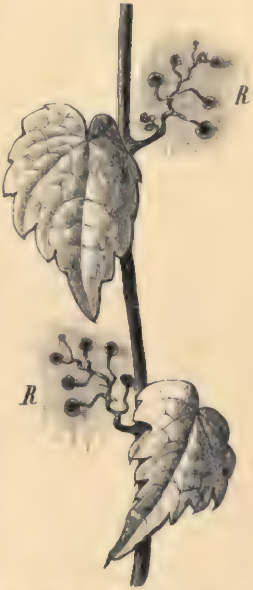


FIG. 29.—*Ampelopsis Veitchii.* *R*, *R*, Stem-tendrils. (¾ nat. size.)

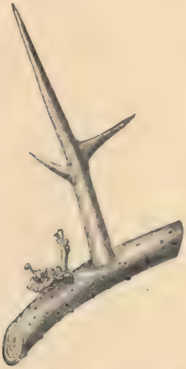


FIG. 30.—Stem-thorn of *Gleditschia triacanthos.* (½ nat. size.)

Tendrillar Shoots.—A peculiar form of metamorphosis is exhibited by some climbing plants through the transformation of certain of their shoots into TENDRILS. Such tendrils assist the parent plant in climbing, either by twining about a support or otherwise holding fast to it. The twining bifurcated tendrils of the Grape-vine, for example, are modified shoots. In some sub-species of the wild vine (*Ampelopsis hederacea*) and in other species of the genus, *e.g. Ampelopsis Veitchii* (Fig. 29), the tendrils are able to form adhesive discs at the tips of the branches, and thus to cling to flat supports.

Stem-thorns.—Shoots may undergo a still greater reduction by their modification into THORNS, as a defence against the depredations of animals. Of shoots modified in this manner, the Black Thorn (*Prunus spinosa*), the White Thorn (*Crataegus*), and the Honey Locust (*Gleditschia*) afford instructive examples. The thorns are simple or branched, hard, pointed bodies. In *Gleditschia* (Fig. 30) the thorns are developed primarily from the uppermost of several serial buds; while secondary thorns may develop on older portions of the stem from the lower buds of the series, and thus give rise to clusters of thorns. In *Colletia cruciata* all the shoots are flattened and spiny, so that they perform the duties of the leaves, which are quickly lost, in addition to serving as protective structures. This plant is an American shrub belonging to the Rhamnaceae, and grows in dry sunny situations.

Flowers.—The most marked changes in the form of the shoot, due to the displacement and union of its different members, take place in phanerogamic flowers (Fig. 39). The shoots from which flowers are developed are termed FLORAL SHOOTS, in contrast to the FOLIAGE SHOOTS, the functions of which are merely vegetative. The axis of the floral shoot remains short, and becomes flattened or even depressed at the tip. The leaves which spring from the floral axis often become united with one another and with the axis itself. In such cases thorough investigation of the development and the comparative morphology of the flower is necessary to reveal the modifications which have taken place during its evolution. In most instances the rule seems to hold that axillary buds are not formed within a flower except in cases of abnormal development.

The Order of Sequence of Shoots.—If the vegetative cone of the primary axis of a plant, after reaching maturity, is capable of reproduction, a plant with but one axis will result, and the plant is designated UNIAXIAL or HAPLOCAULESCENT. Usually, however, it is not until a plant has acquired axes of a second or third order, when it is said to be DIPLOCAULESCENT or TRIPLOCAULESCENT, or of the *n*th order, that the capacity for reproduction is attained. A good illustration of a plant with a single axis is afforded by the Poppy, in which the first shoot produced from the embryo terminates in a flower, that is, in that organ of Phanerogams which includes the sexual organs. As an example of a triplocaulescent plant may be cited the common Plantain (*Plantago major*), whose primary axis produces only foliage and scale leaves; while the secondary axes give rise solely to bracteal leaves, from the axils of which finally spring the axes of the third order, which terminate in the flowers. In the case of trees, only shoots of the *n*th order can produce flowers. Thus a division of labour commonly occurs in a branched plant, which finds its expression in differences of form between the successive shoots. These differ in appearance according to the special function performed by them, whether nutrition, storage, or reproduction. In addition to the essential members in the succession of shoots developed in a determined order, there are non-essential members which repeat forms of shoot already present. These may appear simultaneously with the essential shoots, and serve to increase the size of the plant as in many annuals; in many perennial plants they arise as yearly innovations on the stock. Adventitious shoots, as a rule, repeat members which have already made their appearance. Exceptionally, they form necessary links in the succession of shoots; this is the case in the Podostemaceae (an aquatic order of Dicotyledons found in the tropics, the plants belonging to which resemble Lichens or Liverworts in external form), where they bear the flowers.

The Habit or General Aspect of Plants is dependent upon the origin, number, mode of growth, and duration of their branches, and on the presence or absence of non-essential shoots. Cormophytes which develop herbaceous aerial shoots, and persist only so long as is requisite for the development and ripening of their fruit, be it one or several vegetative periods, are called HERBS. Herbaceous plants, however, which, although annually dying down to the ground, renew their existence each year by means of new shoots produced from underground shoots, rhizomes, or roots, are further distinguished as PERENNIALS or perennial herbs. SHRUBS or TREES, on the other hand, have woody, persistent shoots, which bear fruit repeatedly. In these the reproductive shoots are shed annually, and, in some, vegetative branches are also cast off, the remaining ones persisting and increasing in thickness. In the Lime the ends of the leafy twigs, in the Scotch Fir the short shoots, and in the Oak, Elm, Willow, and Poplar weak lateral branches are thus lost. The leaves of evergreen trees remain alive for several years, while those of deciduous species only persist for a single vegetative period.

Shrubs retain their lateral shoots, so that their branches are formed near the ground; trees, on the contrary, soon lose their lower lateral branches, and have a main stem or trunk, which bears a crown of branches and twigs. In many trees, shrubs, and herbs the main shoot is vertical, while the lateral branches assume a horizontal position, or are directed obliquely upwards or downwards. In other cases the main axis is sympodial, a lateral branch continuing the direction of growth of the primary shoot. Sometimes a main axis is indistinguishable among the group of similarly directed branches. The general appearance of the plant is determined by the direction and thickness of its branches and leafy twigs. If these are all directed upwards the shape is pyramidal, while broadly pyramidal, oval, and rounded forms arise when the branches diverge more strongly. The "weeping varieties" of several familiar trees are due to the branches becoming long and pendulous. Herbaceous plants often have stems which creep on the surface of the ground. Other plants, both herbaceous and woody, climb upon various supports by means of hooked hairs, prickles, and modified shoots, by means of roots or tendrils, or by twining movements. Climbing plants are termed LIANES, those which wind round a support being distinguished as TWINING PLANTS. It is the presence of numerous rope-like stems of lianes which renders the tropical forest so impenetrable. On both creeping and climbing shoots the leaves tend to become displaced towards the dorsal surface of the stem, while branches spring from the sides and roots from the ventral surface.

In catalogues and descriptions of plants the duration of the period of growth is usually expressed by special symbols : thus ⊙ indicates an annual ; ⚇ a biennial, and ♃ a perennial herb ; ♄ is employed to designate both trees and shrubs, and for trees the sign ♄ is also in use.

Development of the Leaf.—The first appearance of the leaf as a lateral protuberance (Fig. 17 *f*) on the vegetative cone of the shoot has already been referred to (p. 18). When the apex of a shoot is removed by a transverse section and viewed from above (Fig. 31), the origin of leaves as lateral protuberances is more evident than in a longitudinal section. The embryonic leaf rudiment generally occupies but a small portion of the periphery of the vegetative cone ; it may, however, completely surround it. In like manner, when the mature leaves are arranged in whorls, the developing protuberances of the rudimentary leaves may form at first a continuous wall-like ring around the growing point and only give rise later to the separate leaf rudiments. Leaves take their origin only from such parts of a plant as have remained in an embryonic condition. A leaf never arises directly from the older parts of a plant. In cases where it apparently does so its development has been preceded by the formation of a growing point of a new shoot. The growing point of a shoot has usually an UNLIMITED GROWTH, while the growth of a leaf is LIMITED. A leaf usually continues to grow at its apex for a short time only, and then completes its segmentation and development by intercalary growth, which is usually localised near the base. It is true that some leaves, such as those of Ferns, have apical growth and continue to grow for a long time (in some cases, *e.g. Lygodium*, the growth is unlimited), and bear their pinnae in acropetal order. On the other hand, the leaf-like cladodes, although they are in reality

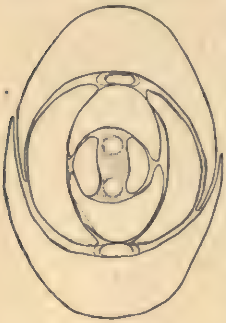


FIG. 31.—Apical view of the vegetative cone of a shoot of *Euonymus japonicus*. (× 12.)

metamorphosed shoots, exhibit a limited apical growth like that of ordinary leaves.

We have already seen that in certain cases the apical cone may give rise to a terminal leaf. The apex of the leaf in many ferns (*e.g. Adiantum Edgeworthii*) may on the other hand be transformed into a bud from which a shoot will develop (13).

The unsegmented protuberance of the still rudimentary leaf, termed by EICHLER (14) the primordial leaf (Fig. 32 *A b*), first projects from the vegetative cone of the shoot (*A v*). This is usually followed by a separation of the primordial leaf into the LEAF-BASE (*g* in *A* and B) and the rudimentary lamina or UPPER LEAF (*o* in *A* and *B*). The leaf-base, or the part of the rudimentary leaf which immediately adjoins the vegetative cone, either takes no further part in the succeeding differentiation of the leaf, or it develops into a LEAF-SHEATH (vagina) or into STIPULES. The upper leaf, on the other hand, gives rise to the leaf-blade or LAMINA. If the fully developed leaf possesses a LEAF-STALK (petiole), this is later interposed by intercalary growth between the leaf-blade and the leaf-base.

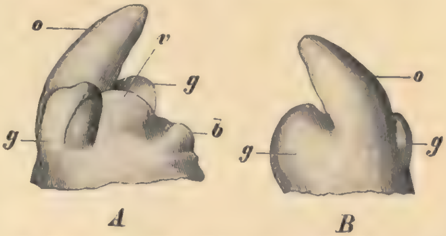


FIG. 32.—Apex of an Elm shoot, *Ulmus campestris*. *A*, Showing the vegetative cone *v*, with the rudiments of a young leaf, *b*, still unsegmented, and of the next older leaf, exhibiting segmentation into the laminar rudiment, *o*, and leaf-base, *g*; *B*, showing the older leaf, viewed obliquely from behind. (× 58.)

The leaf-tip often develops more rapidly than the rest of the leaf, and GOEBEL regards this as an arrangement for the protection of the younger parts of the bud (15). This is seen most strikingly in some tropical plants, especially in climbers. In this case, according to M. RACIBORSKI (16), the "fore-runner tips" serve for assimilation before the remainder of the leaf has attained the mature condition.

In leaves the laminae of which do not remain simple, but undergo segmentation as they develop, the lateral segments are as a rule formed in the basipetal direction, *i.e.* from the tip towards the base (Fig. 33); the opposite direction of development is, however, sometimes found. The segments of the palmate and pinnate leaves of Palms originate by a process of splitting of the leaf blade which is, to begin with, entire. The direction of the splits is determined by the folds of the lamina (17).

Different forms of leaves are most clearly seen in the Phanerogams, in which the various leaf structures found at different regions of the shoot have been distinguished as SCALE LEAVES, FOLIAGE LEAVES, BRACTEAL LEAVES, and FLORAL LEAVES (Fig. 34). These usually succeed one another in definite order. However unlike the leaves may become, their first origin is similar. Since the scale leaves and bracts can often be shown to be arrested forms of foliage leaves, the latter may be first considered.

Foliage Leaves, generally referred to simply as leaves, are the leaf structures on which devolves the task of providing nourishment for the plant. Since the exercise of this function is dependent upon the presence of the green pigment, foliage leaves have a green colour. In certain cases, where their form is extremely simple, as in the needles of Conifers, the primordial leaf simply increases in length without any further differentiation into parts. In other undivided leaves, however, whether lanceolate, elliptical, ovate, or otherwise shaped, the flat leaf-blade is distinct from the leaf-base, while a leaf-stalk may also be interpolated between them. If no leaf-stalk is developed the leaf is said to be SESSILE, otherwise it is described as STALKED.

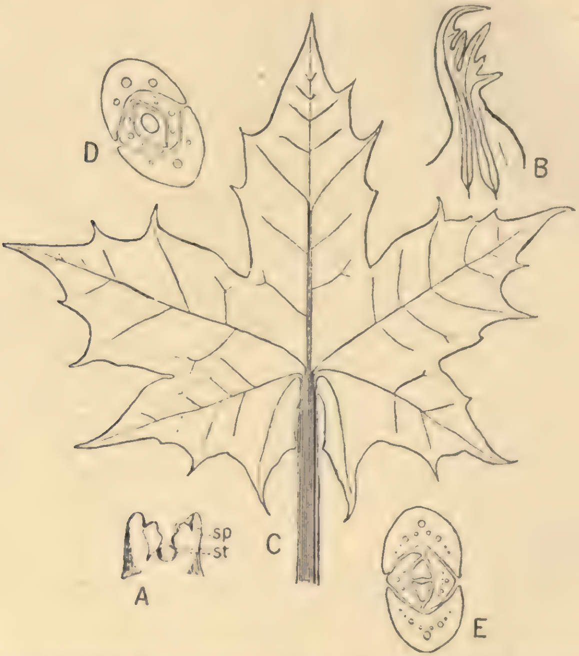


FIG. 33.—*Acer platanoides*. *A*, external view of a bud, with two young leaves between which the apical cone of the stem is visible; *sp*, the leaf-blade, in which five segments are indicated, the uppermost one being developed first; *st*, the zone, by the growth of which the leaf-stalk will arise later. *B*, an older leaf seen from the side; the young vascular bundles, which will later determine the venation, are indicated. *C*, fully-grown leaf, with the course of the vascular bundles indicated diagrammatically. *D*, a transverse section of the basal portion of a bud showing three vascular bundles in each leaf. *E*, a similar section at a higher level; the number of vascular bundles has increased by branching. (After DEINEGA, from GOEBEL'S *Organography*. *A*, *B*, and *E* slightly magnified.)

Sessile leaves usually clasp the stem by a broad base. Where, as in the case of the Poppy (*Papaver somniferum*), the leaf-base surrounds the stem, the leaves are described as AMPLEXICAUL; if, as in species of *Bupleurum*, it completely surrounds the stem, the term PERFOLIATE is used. If the bases of two opposite leaves are united, as in the Honeysuckle (*Lonicera Caprifolium*), they are said to be CONNATE. Where the blade of the leaf continues downwards along the stem, as in the winged stems of the common Mullein (*Verbascum thapsiforme*), the leaves are distinguished as DECURRENT. The petiole of a leaf merges either directly into the leaf-base, or it swells at its lower end into a LEAF-CUSHION or PULVINUS, and is thus articulated with the leaf-base. This is the case, for instance, with many of the Leguminosae. The leaf-blade, in turn, may be either sharply marked off from the petiole, or it may be prolonged so that the petiole appears winged, or again it may expand at its junction with the petiole into ear-like lobes. A leaf is said to be ENTIRE if the margin of the leaf-blade is wholly free from indentations, or if the latter are very shallow. When the incisions are deeper, but do not extend half-way to the middle of the leaf-blade, a leaf is distinguished as LOBED; when they reach more than half-way, as CLEFT (Fig. 35 *sb*); if the incisions are still deeper the leaf is said to be PARTITE (Fig. 38 *l*), and if they penetrate to the midrib or base of the leaf-blade it is termed DIVIDED. The divisions of the leaf-blade are said to be PINNATE or PALMATE, according as the incisions run towards the midrib or towards the base of the leaf-blade. Where the divisions of the leaf-blade are distinct and have a separate insertion on the common leaf-stalk or on the midrib, then termed the SPINDLE or RHACHIS, a leaf is spoken of as COMPOUND (Fig. 35 *ub*); in all other cases it is said to be SIMPLE. The single, separate divisions of a compound leaf are called leaflets. These leaflets, in turn, may be entire, or may be divided and undergo the same segmentation as single leaves. In this way double and triple compound leaves may be formed. Simply and doubly PINNATE leaves in which the leaflets are attached to the two sides of the rhachis are of common

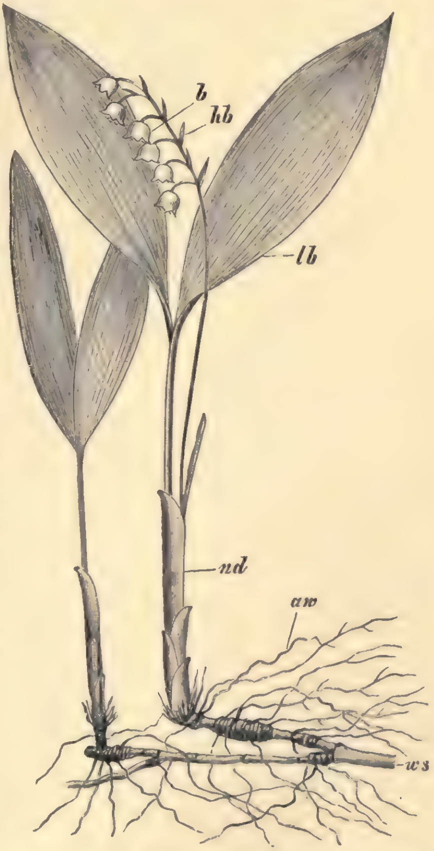


FIG. 34.—Lily of the Valley (*Convallaria majalis*). *nd*, Scale leaves; *lb*, foliage leaves; *hb*, bracts; *b*, flower; *ws*, rhizome; *aw*, adventitious roots. (Somewhat reduced.)

occurrence. The leaflets are either sessile or stalked; and sometimes also, as in *Robinia* and *Mimosa*, their stalks articulate with the spindle by means of swollen pulvini. The term PEDATE is applied to leaves in which the segments are further divided on one side only, and the new segments are similarly divided (Fig. 38 *l*). Variations in the outline of leaves, whether they are entire, serrate, dentate, crenate, incised, etc., as well as peculiarities in their shape and segmentation, are of use in the determination of plants.

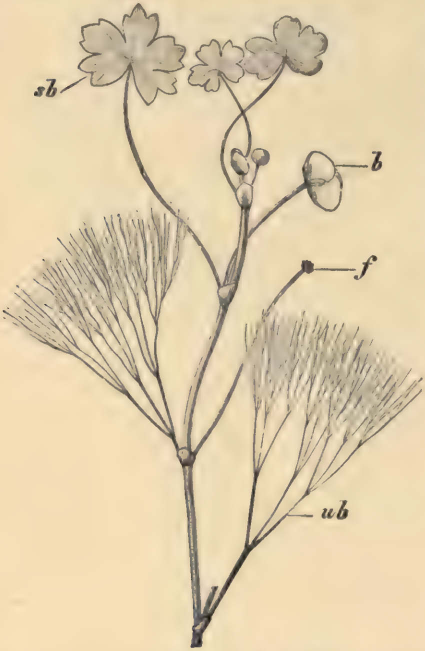


FIG. 35.—*Ranunculus aquatilis.* *ub*, Submerged leaves; *sb*, floating leaves; *b*, flower; *f*, fruit. (Reduced.)

A system of strands known as the VEINS or NERVES, traverses the flat leaf-blade. They project more or less from the surface, especially on the lower side where they often form definite ribs. Frequently the nerve in the median line of the lamina is more strongly developed and is then termed the midrib; in other cases several equally developed main nerves are present. Lateral nerves spring from the one or more main nerves.

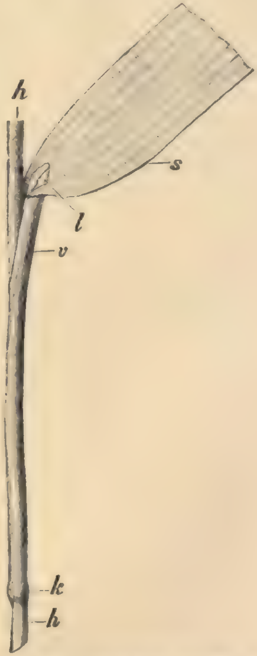


FIG. 36.—Part of stem and leaf of a grass. *h*, Haulm; *v*, leaf-sheath; *k*, swelling of the leaf-sheath above the node; *s*, part of leaf-blade; *l*, ligule. (Nat. size.)

According to their VENATION OF NERVATURE leaves are described as PARALLEL VEINED OR NETTED VEINED. In parallel venation the veins or nerves run either approximately parallel with each other or in curves, converging at the base and apex of the leaf (Fig. 36 *s*); in netted veined leaves (Fig. 190) the veins branch off from one another, and gradually decrease in size until they form a fine anastomosing network. In leaves with parallel venation the parallel main nerves are usually united by weaker cross veins. Netted or reticulately veined leaves in which the side veins run from the median main nerve or MIDRIB are further distinguished as PINNATELY VEINED, or as PALMATELY VEINED when several equally strong ribs separate at the base of the leaf-blade, and give rise in turn to a network of weaker veins. Parallel venation is characteristic, in general, of the Monocotyledons; reticulate venation, of Dicotyledons. Monocotyledons have usually simple leaves, while the leaves of Dicotyledons are often compound, and are also more frequently provided with stalks.

The nerves or veins give to a leaf its necessary mechanical rigidity and render possible its flattened form. The branches of the veins parallel to the margin of most leaves prevent their tearing: when there are no such marginal nerves in large thin leaves, the lamina is easily torn into strips by the wind and rain. This frequently happens to the leaves of the Banana (*Musa*), which, consequently, when growing under natural conditions in the open air, presents quite a different appearance from what it does when grown under glass. The leaves of the Banana, after becoming thus divided, offer less resistance to the wind. In a similar manner the leaves of Palms, although undivided in their bud state, become torn even during the process of their unfolding. A similar protection from injury is afforded to the Aroid (*Monstera*) by the holes with which its large leaf-blades become perforated. Equally advantageous results are secured by many plants whose leaves are, from their very inception, divided or dissected. The submerged leaves of aquatic plants, on the other hand, are generally finely divided, not only for mechanical purposes, but also to afford a more complete exposure of the leaf surface to the water. Accordingly, in such water-plants as *Ranunculus aquatilis* (Fig. 35), which possess both floating and submerged leaves, it is generally the latter only that are dissected and filiform in character. The pointed extremities (DRIP TIPS) of the foliage leaves of many land plants, according to STAHL (18), facilitate the removal of water from the leaf surface. Fleshy so-called succulent leaves, like fleshy stems, serve as reservoirs for storing water.

Heterophylly.—Many plants are characterised by the development of different forms of foliage leaves. Such a condition is known as heterophylly. Thus the earlier leaves of *Eucalyptus globulus* are sessile and oval, while those subsequently formed are stalked and sickle-shaped. In other cases the heterophyllous character of the leaves may represent an adaptation to the surrounding environment, as in the Water Crowfoot (*Ranunculus aquatilis*), in which the floating leaves are lobed, while those entirely submerged are finely divided (Fig. 35). A number of epiphytic Ferns belonging to the genera *Polypodium* and *Platycerium* alternately bear stalked, pinnate leaves serving for assimilation, and broad, sessile, usually cordate NEST-LEAVES which serve to collect humus; when, as MANTLE-LEAVES, they are closely appressed to the substratum they form humus by their rapid decay. The humus thus collected or produced is penetrated by the roots of the Fern (19).

The Leaf-base.—In Monocotyledons the leaf-base very often forms a SHEATH about the stem; in Dicotyledons this happens much less frequently. In the case of the Gramineae, the sheath is open on the side of the stem opposite the leaf-blade (Fig. 36 *v*), while in the

Cyperaceae it is completely grown together. The sheath of the Grasses is prolonged at the base of the lamina into a scaly outgrowth, the ligule (*l*). Such a sheath, while protecting the lower part of the internodes, which remain soft and in a state of growth, gives them at the same time rigidity. STIPULES are lateral appendages sometimes found at the base of leaves. When present they may be either small and inconspicuous (Fig. 37 *nb*), or may attain a considerable size. When their function is merely to protect the young growth in the bud, they are usually of a brown or yellow colour, and are not persistent; whereas, if destined to become assimilatory organs, and to assist in providing nourishment, they are green, and may assume the structure and form of the leaf-blade, which sometimes becomes modified and adapted to other purposes (Figs. 48, 49). Normally, the stipules are two in number, that is, one on each side of the petiole. In many species of *Galium*, where the stipules resemble leaf-blades, the leaf-whorls appear to be composed of six members, but consist actually of but two leaves with their four stipules, which may be easily distinguished by the absence of any buds in their axils. In other species of the same genus (*Galium cruciatum* and *palustre*) there are only four members in the whorls, as each two adjoining stipules become united. In many cases, as in the Rose and the Clover, the stipules have the form of appendages to the enlarged leaf-base. Sometimes both stipules are united into a single one, which then appears to have an axillary

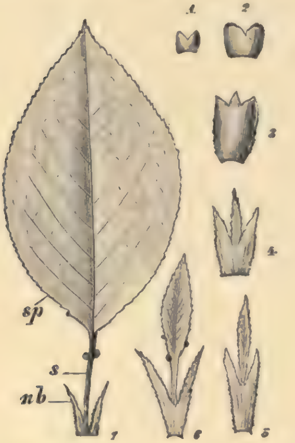


FIG. 37.—Bird Cherry (*Prunus Avium*). Bud-scales (1-3) and the transition forms (4-6) to the foliage leaf (7); *sp*, leaf-blade; *s*, leaf-stalk; *nb*, stipules. (Reduced slightly.)

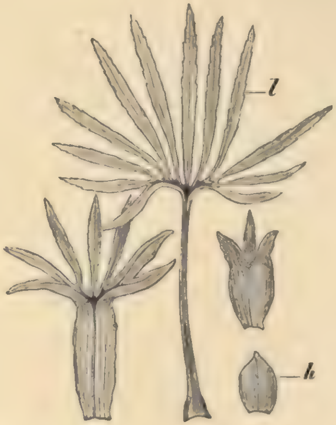


FIG. 38.—*Helleborus foetidus*. Foliage leaf (*l*) and intermediate forms between this and the bract (*h*). (Reduced.)

origin; or the stipules may completely encircle the stem, and thus form a sheath (OCHREA) about the younger undeveloped leaves. This sheath-like fusion of the stipules may be easily observed on the India-rubber tree (*Ficus elastica*), now so commonly grown as a decorative plant. In this case the stipular sheath is burst by the unfolding of each new leaf and pushed upwards. In the Polygonaceae the stipular covering is similarly torn apart by the developing leaves, but remains on the stem in the form of a membranous sheath.

Scale Leaves possess a simpler form than foliage leaves, and are attached directly to the stem, without a leaf-stalk. They exercise no assimilatory functions, and are more especially of service as organs of protection. Scale leaves exercise their most important function as BUD-SCALES (Fig. 37); they are then hard and thick, and usually of a brown colour. They most frequently take their origin from the enlarged leaf-base; in that case the upper leaf either does not develop, or exists only in a reduced condition at the apex of the scale. The true morphological value of scale leaves of this nature is very evident in the bud-scales of the winter buds of the Horse-chestnut (*Aesculus Hippocastanum*); for, while the outer scales show no perceptible indications of an upper leaf, small leaf-blades can be distinctly distinguished at the apices of the inner scales. In other cases the scale leaves are modified stipules (Fig. 37), and are then also derived from the leaf-base; while, in other instances, they correspond to the enlarged, but still undifferentiated, primordial leaves. The bud-scales of the Oak are the stipules of leaves of which the laminae are only represented by minute scales. Scale leaves, usually colourless and in various stages of reduction, are found on rhizomes (Figs. 23, 34), bulbs (Fig. 25), and tubers (Fig. 26). On the aerial stems arising from such subterranean shoots the formation of similar scale leaves generally precedes the development of the foliage leaves, with which they are connected by a series of transitional forms.

Bracteal Leaves resemble scale leaves in form, and have a similar origin (Fig. 34 *hb*). They act as subtending leaves for the floral shoots, and are termed BRACTS. They are connected with foliage leaves by intermediate forms (Fig. 38). Though they are not infrequently green they may be otherwise coloured, or even colourless.

Floral Leaves.—The modified leaves which form the flowers of Phanerogams are termed floral leaves. In the highest development attained by a phanerogamic flower (Fig. 39), the successive floral leaves are distinguished as sepals (*k*), petals (*c*), stamens (*a*), and carpels (*g*). In form the sepals and petals approach the bracts. In most cases the sepals are green and of a firm structure; the petals, on the other hand, are more delicate and variously coloured.

The stamens are generally filamentous in shape, and produce the pollen in special receptacles. The carpels more closely resemble scale leaves, and in Angiosperms by closing together form receptacles within which the ovules are produced. The stamens and carpels of Phanerogams correspond to the spore-bearing leaves of the Vascular Cryptogams. Such spore-bearing leaves are termed SPOROPHYLLS, and even in the Vascular Cryptogams exhibit a greater or less departure from the form of other foliage leaves.

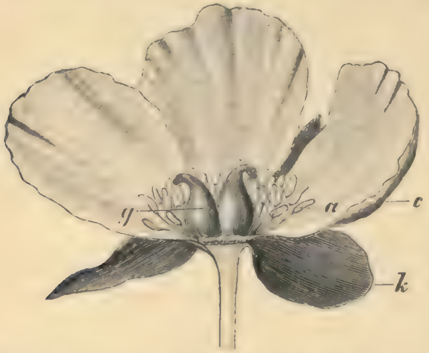


FIG. 39.—Flower of *Paeonia peregrina*. *k*, Sepals; *c*, petals; *a*, stamens; *g*, carpels. Some of the sepals, petals, and stamens have been removed to show the pistil, consisting of two separate carpels. (Half nat. size.)

It is evident that the scale and bracteal leaves are to be considered as rudimentary foliage leaves, not only from the mode of their development but also from the possibility of transforming them into foliage leaves. GOEBEL, by removing the growing tip and foliage leaves of a shoot, succeeded in forcing it to develop other foliage leaves from its scale leaves (^{20}). Rhizomes, grown in the light, develop foliage leaves in place of the usual scale leaves, and even on a potato it is possible to induce the formation of small foliage leaves instead of the customary scale leaves.

Leaf-Scars.—After a leaf has fallen, its previous point of insertion on the stem is marked by the cicatrix or scar left by the fallen leaf. In winter, accordingly, when the trees are denuded of their leaves, the axillary buds are seen to be situated above the leaf-scars.

Vernation and Æstivation.*—A section through a winter bud shows a wonderful adaptation of the young leaves to the narrow space in which they are confined. They may be so disposed that the separate leaves are spread out flat, but more frequently they are folded, rolled (Fig. 40 *l*), or crumpled. The manner in which each separate leaf is disposed in the bud is termed VERNATION. On the other hand, the arrangement of the leaves in the bud with respect to one another is designated ÆSTIVATION. In this respect the leaves are distinguished as FREE when they do not touch, or VALVATE when merely touching, or IMBRICATED, in which case some of the leaves are overlapped by others (Fig. 40 *k*). If, as frequently occurs in flower-buds, the margins of the floral leaves successively overlap each other in one direction, the æstivation is said to be CONTORTED.

---

* [The use of these terms in the following paragraph differs from that customary in England. By VERNATION is understood the arrangement of the leaves in a vegetative bud as a whole. The folding of each individual leaf in the bud is termed PTYXIS. The term ÆSTIVATION is applied to the arrangement of the parts in a flower-bud.—TRANS.]

The Arrangement of Leaves.—In all erect elongated shoots, and still more so in dwarf shoots, it is apparent that there is a marked regularity in the arrangement of leaves. This regularity may be most easily recognised in cross-sections of buds (Fig. 41), particularly in sections showing the apex of the vegetative cone (Figs. 31, 33), From such sections it is evident that the developing leaf-rudiments stand in the relative position to the pre-existing leaves which best utilises the available space. According to Schwendener (21) the arrangement of the leaves on the axis is determined by purely mechanical causes; it is dependent on the pressures and tensions induced by the leaves which always stand in contact at their origin. The original arrangement of the young leaves may be modified as growth continues owing to the mutual pressure they exert. If the axis does not grow in length, but only in thickness, as the rudimentary leaves increase in size, their points of insertion will be displaced laterally by longitudinal pressure; if the axis increases in length, and not in thickness, the insertion of the leaves will be displaced by a transverse pressure. The arrangement of the leaves would also be affected by any increase or decrease in the size of the vegetative cone, unaccompanied by a corresponding increase or cessation of the growth of the rudimentary leaves.

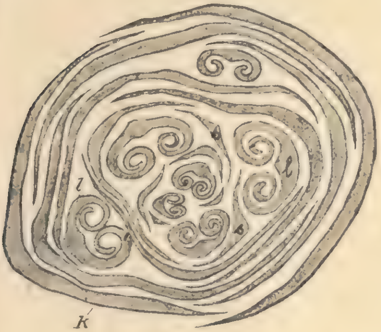


FIG. 40.—Transverse section of a bud of *Populus nigra*. *k*, Bud-scales showing imbricated æstivation [vernation]; *l*, foliage leaves with involute vernation [ptyxis]; *s*, each leaf has two stipules. (× 15.)

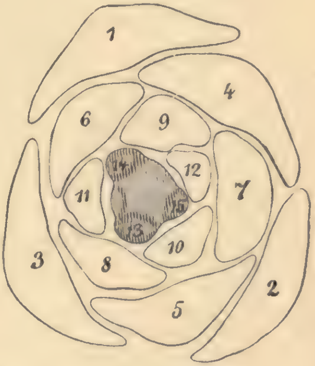


FIG. 41.—Transverse section of a leaf-bud of *Tsuga canadensis*, just below the apex of the shoot, showing a $\frac{5}{13}$ divergence. (After HOFMEISTER.)

In developing flowers sudden changes in the relative position of the parts often occur in which the apical cone undergoes rapid increase in size while the leaf rudiments become smaller. Changes in the usual position of the leaves may also be occasioned by the torsion of their parent stem. Thus the leaves of *Pandanus* first appear in three straight rows on the vegetative cone, and their subsequent spiral arrangement results from the torsion of the stem. Irregular arrangement of the leaves, such as occurs, for example, on the flower-stalk of the Crown Imperial (*Fritillaria imperialis*), may result from the unequal size of the leaves at the time of their inception on the vegetative cone. Further observation has revealed an increasing number of cases in which definite leaf arrangements cannot be explained by the spatial relations, and as the effect of contact and pressure. It can only for the present be assumed that the cause of the leaf-arrangement in these cases lies in the inherited organisation of the plant (22).

A frequent mode of arrangement of foliage leaves is the decussate, in which two-leaved whorls alternate with each other (Figs. 31, 33). A whorled arrangement is characteristic of floral leaves. When the number of leaves in each whorl is the same the whorls usually alternate. On the other hand, the number of members in the different whorls of floral leaves will often be found to change, especially on passing from the petals to the stamens, or from the latter to the carpels. In many cases a whorl, the existence of which would be expected from the position of other whorls and from a comparison with allied plants, may be altogether wanting. In this connection a comparison of the flowers of the Liliaceae and Iridaceae will be instructive. The flowers of the Liliaceae (Fig. 42) are composed of five regularly alternating, three-leaved whorls or cycles, viz. a calyx and a corolla (each consisting of three leaves, and, on account of their similar appearance, usually referred to conjointly as the PERIANTH), an outer and an inner whorl of stamens, and finally, in the centre of the flower, an ovary of three carpels. In the flowers of the Iridaceae (Fig. 43) the arrangement is exactly similar, except that one whorl, that of the inner cycle of stamens, is lacking, but the three carpels are situated exactly as if the missing whorl of stamens were present. From this similarity of arrangement, despite the absence of the one cycle of stamens, the conclusion has been drawn that, at one time, the inner row of stamens was actually present, but has now disappeared. In constructing a THEORETICAL DIAGRAM of the Iridaceae the missing cycle of stamens is indicated by some special sign (by crosses in Fig. 43); a diagram in which theoretical suppositions are not taken into consideration is called an EMPIRICAL DIAGRAM. Diagrams showing the alternate arrangement of leaves, in cases where only a single leaf arises from each node, may be constructed by projecting the

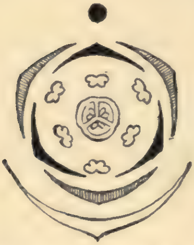


FIG. 42.—Diagram of a Liliaceous flower. The main axis is indicated by a black dot, opposite to which is the bract.

successive nodes of a stem upon a plane by means of a series of concentric circles, on which the position of the leaves may be indicated (Fig. 44). The angle made by the intersection of the median planes of any two successive leaves is called their DIVERGENCE, and is expressed in fractions of the circumference; for example, when the angular divergence between two successive leaves is 120°, their divergence is expressed by the fraction $\frac{1}{3}$. In the adjoining diagram (Fig. 44) a $\frac{2}{5}$ divergence is shown. Where the lateral distance between two successive leaves is $\frac{2}{5}$ of the circumference of the stem, the sixth leaf is above the first, the seventh above the second, and so on. The leaves form on the axis five vertical rows, which are spoken of as ORTHOSTICHIES. Where the leaves are very much crowded, as in dwarf-shoots, a set of spiral rows called PARASTICHIES, due to the contact of the nearest laterally adjacent members, becomes much more noticeable than the orthostichies. If the surface of such an axis be regarded as spread out horizontally, the parastichies become at once distinguishable (Fig. 45), and it will be evident that the sum of the parastichies cut by every cross-section through such an axis must equal the number of the orthostichies. On objects like pine cones, in which the parastichies are easily recognised, they may be used to determine the leaf arrangement. If a line be drawn on the surface of a stem, so as to pass in the

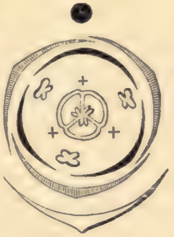


FIG. 43. — Theoretical diagram of the flower of the Iris. The absent whorl of stamens is indicated by crosses.

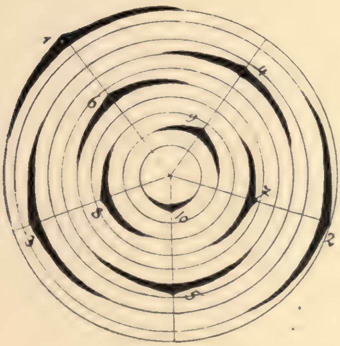


FIG. 44. — Diagram showing $\frac{2}{5}$ position of leaves. The leaves numbered according to their genetic sequence.

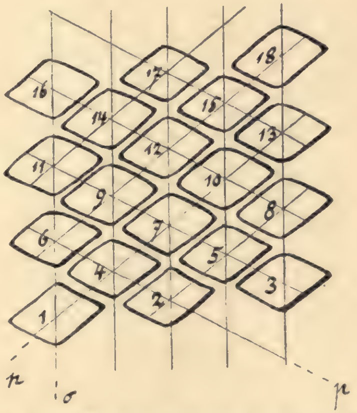


FIG. 45.—The $\frac{2}{5}$ position on the outspread surface of the axis. *o*, Orthostichies; *p*, parastichies. The leaves are numbered according to their genetic sequence.

shortest way successively through the points of insertion of every leaf, a spiral called the GENETIC SPIRAL will be constructed. That portion of the genetic spiral between any two leaves directly over each other on the same orthostichy is termed a CYCLE. Where the divergence is $\frac{2}{5}$, a cycle will accordingly include five leaves, and will in such a case have made two turns about the stem. The most common divergences are the following, $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, $\frac{13}{34}$, etc. In this series it will be observed that in each fraction the numerator and denominator are the sum of those of the two preceding fractions. The value of the different fractions varies accordingly between $\frac{1}{2}$ and $\frac{1}{3}$, while always approaching a divergence angle of 137° 30′ 28″. The great majority of leaf arrangements can be expressed by the terms of this main series of divergences.

This main series was discovered by CARL SCHIMPER and ALEXANDER BRAUN. It exhibits a rational relation of the divergences to the circumference of the axis, so that, as the number of leaves increases, definite leaves are situated accurately above one another. As WIESNER (23) in particular has made clear, it differs from all other possible series in attaining the most equal distribution of the leaves on the axis bearing them, while requiring the smallest number of leaves. This results in an advantageous utilisation of the available space, a well-distributed loading of the axis and, when the latter is vertical, in the best utilisation of the illumination. The importance of these advantages as determining the leaf-arrangement is seen in those cases in which a plant bears only a few (2-4) leaves. These stand in a whorl at equal distances from one another and thus their weight is equally distributed, and they obtain equal amounts of light. When leaves are arranged alternately on a vertical axis, their size and shape, together with the length of the internodes, ensure each obtaining the requisite amount of light. This arrangement is not a convenient one, and as the leaves borne on a vertical axis increase in number their divergence becomes progressively higher. It is otherwise in inclined or horizontal axes; here the divergence is relatively low, usually $\frac{1}{2}$ or an approximation to this, since this corresponds to the most favourable exposure of the leaves to the light. In most instances this advantageous result is attained by twisting of the internodes; thus when, as is often the case, the leaves are decussate on an erect axis, they form four vertical rows; but when it is inclined they are brought by twisting to stand in two rows. Similar secondary changes exposing the leaf-blades to the light affect alternately arranged leaves. The position of the foliage leaves is indeed always clearly adapted to the need of illumination. When the leaves form a rosette, the stalks of those lowest on the stem are frequently elongated, so that their blades are not shaded by the more central leaves. This is especially well seen in the floating rosettes of *Trapa natans*.

While the arrangement of the foliage leaves conforms on the whole to the main series of divergences, this is not usually suitable in the case of the foliar structures of flowers and inflorescences, which have different purposes to serve. Other relations of position also occur in the vegetative region, as has been shown by GOEBEL (24), in particular in the case of dorsiventral shoots. The tips of dorsiventral shoots are frequently coiled ventrally inwards, bearing their leaves either dorsally or on the sides, but, in the latter case, approaching the dorsal surface. The creeping stems of many Ferns or the flower-bearing shoots of

Forget-me-not (*Myosotis*) are good examples of such dorsiventral shoots. The line joining successive leaves in such case is, at the best, but a zigzag. On the ground of such observations as these it may be concluded that the actual leaf-arrangements represent adaptations to definite conditions of life, and that with alterations in the latter other arrangements must arise.

The Metamorphosis of Foliage Leaves.—A striking modification of foliage leaves is seen in peltate leaves, in which the petioles are attached to the lower surfaces somewhat within the margin, as in the leaves of the Indian Cress (*Tropaeolum majus*, Fig. 191). In the process of their development the young leaf-blades, in this case, grow not only in the same direction as the petioles, as a prolongation of them, but also horizontally in front of them. The tubular leaves of many insectivorous plants may have commenced their development in much the same way. The leaves of *Nepenthes robusta* (Fig. 46), for example, in the course of adaptation to the performance of their special function, have acquired the form of a pitcher with a lid which is closed in young leaves, but eventually opens. The pitcher, as GOEBEL has shown, arises as a modification of the leaf-blade. At the same time the leaf-base becomes expanded into a leaf-like body, while the petiole between the two parts sometimes fulfils the office of a tendril. By a similar metamorphosis of its leaflets, bladder-like cavities are developed on the submerged leaves of *Utricularia* (Fig. 47). The entrance to each bladder is fitted with a small valve which permits the ingress but not the egress of small water-animals. While such leaves display a progressive metamorphosis the modification may be of the nature of a reduction, as is the case in many Ferns, which form leaf-runners. Like the modified

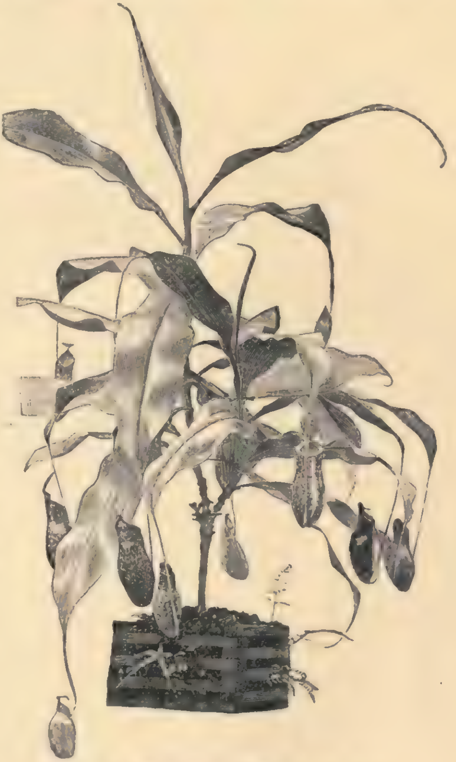


FIG. 46.—*Nepenthes robusta.* ($\frac{1}{8}$ nat. size.)

shoots of the same name these are elongated and enable the bud produced at the end to develop at a distance from the parent plant. *Camptosorus rhizophyllus*, an American Fern, is commonly known as the Walking Fern. Such leaf-runners usually lose their pinnae and are reduced to the leaf stalk. A particularly striking appearance is presented in those cases in which the first leaf of the bud in its turn forms a leaf-runner, so that a sympodium of runners results (*Asplenium obtusifolium*, *A. Mannii*).

A metamorphosis of the whole leaf lamina, or a part of it, into tendrils (LEAF-TENDRILS) is of comparatively frequent occurrence, especially among the Papilionaceae. In the leaf of the Pea (Fig. 48), the leaflets of the upper pairs have become transformed into delicate tendrils which have the power of twining about a support. In the case of the yellow Vetchling, *Lathyrus Aphaca* (Fig. 49), the whole leaf is reduced to a tendril and the function of the leaf-blade is assumed by the stipules (*n*). A comparison between these two forms is phylogenetically instructive, as it indicates the steps of the gradually modifying processes which have resulted in the complete reduction of the leaf lamina of *Lathyrus*. The comparison of the two preceding cases with *Ampelopsis* (Fig. 29) will make the distinction between these tendrils and stem-tendrils clear, and indicate the value of comparative morphological investigation.

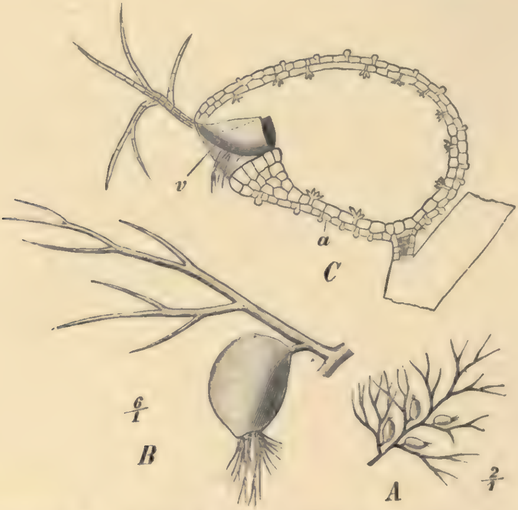


FIG. 47.—*Utricularia vulgaris*. *A*, Part of leaf with several bladders (× 2). *B*, Single pinnule of leaf with bladder (× 6). *C* (after GOEBEL), Longitudinal section of a bladder (× 28): *v*, valve; *a*, wall of bladder.

In *Lathyrus Aphaca* the stipules assume the function of the metamorphosed leaf laminæ; in other instances, as in the case of the Australian species of *Acacia* (Fig. 171, 7, 8, 9), it is the leaf petioles which, becoming flattened and leaf-like in appearance, supply the place of the undeveloped leaf-blades. Such a metamorphosed petiole is called a PHYLLODE, and, except that it is expanded perpendicularly, closely resembles a cladode. From the latter, however, it is morphologically different, for the one represents a metamorphosed petiole, the other a metamorphosed shoot. In accordance with this distinction phyllodes do not, like cladodes, spring from the axils of leaves. Just as stems become modified into thorns (Fig. 30), by a similar metamorphosis leaves may be converted into LEAF THORNS. Whole leaves on the main axis of the Barberry (*Berberis vulgaris*) become thus transformed into thorns, usually three, but in their character of leaves still subtend axillary shoots provided with foliage leaves. By a similar metamorphosis, the two stipules of the leaves of the common Locust (*Robinia Pseudacacia*) become modified into thorns, while the leaf lamina persists as a foliage leaf (Fig. 50).

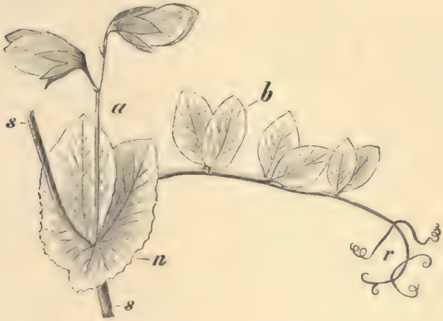


FIG. 48.—Portion of stem and leaf of the common Pea, *Pisum sativum*. *s*, Stem, ; *n*, stipules; *b*, leaflets of the compound leaf; *r*, leaflets modified as tendrils; *a*, floral shoot. (½ nat. size.)

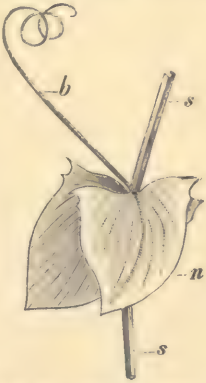


FIG. 49.—*Lathyrus Aphaca*. *s*, Stem; *n*, stipules; *b*, leaf-tendril. (½ nat. size.)

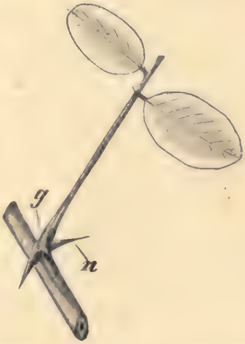


FIG. 50.—Part of stem and compound leaf of *Robinia Pseudacacia*. *n*, Stipules modified into thorns; *g*, pulvinus. (½ nat. size.)

The Root

The third primary member of the cormophytic plant in its typical development as an underground root presents less marked differences in external form than were shown by the other members. This may be put in relation with the uniform conditions to which roots are exposed in the soil. Certain differences are, however, found between the roots of plants adapted to live in different situations (25). The root has as its most important function the absorption of water and nutrient substances dissolved in it from the soil, and also serves to attach the plant firmly in the soil. Frequently it serves for storage of assimilated substances. The general appearance of an underground root differs as it is more specially adapted to perform one or other of these functions. Those roots which grow in water or mud become more elongated, are little branched, and are often provided with special arrangements for aeration which lead to localised swellings; they do not, however, undergo any fundamental change of form. Those roots which grow in the air, AERIAL ROOTS, tend to be more strikingly modified.

The absence of leaves and the existence of a root-cap protecting the growing point are characteristic of roots, and furnish an easy means of distinguishing them from underground shoots. A ROOT-CAP or CALYPTRA affords the vegetative cone of a root the protection that is provided to the apex of a stem by the leaves of the bud. Although, generally, the existence of a root-cap is only disclosed by a median, longitudinal section through the root-tip, in some roots it is plainly distinguishable as a cap-like covering. The very noticeable caps on the water roots of Duckweed (*Lemna*) are not, in reality, root-caps, as they are not derived from the root, but from a sheath which envelops the rudimentary root at the time of its origin. They are accordingly termed ROOT-POCKETS. As a general rule, however, roots without root-caps are of rare occurrence, and in the case of the Duckweed the root-pockets perform all the functions of a root-cap. The short-lived root of the Dodder (p. 27) affords another example of a root devoid of a root-cap. Characteristic of roots are also the ROOT-HAIRS (Fig. 170, *r*), which are found at a short distance from their tips. As the older root-hairs die at the same rate that the new ones are developed, only a small portion of a root is provided with root-hairs at the same time. In some few instances roots develop no root-hairs; this is true of the roots of many Conifers.

Branching of the Root.—Just as the shoot may become bifurcated by the division of its growing point (Fig. 18), so a root may become similarly branched. For the most part, this mode of branching takes place only in the roots of Lycopodiaceae, the shoots of which are also dichotomously branched (p. 19). The branches of roots usually occur in acropetal succession, but the lateral roots (Fig. 170 *w*) make their appearance at a much greater distance from the growing point of the main root than lateral shoots from the apex of their parent stem. By reason of the internal structure of their parent root, lateral roots always develop in longitudinal rows (Fig. 170). They are of endogenous origin, and before reaching the surface must break through the surrounding and overlying tissue of the parent root, by the ruptured portions of which they are often invested at the base, as with a collar.

ADVENTITIOUS ROOTS, just as adventitious shoots, may arise from any part of a plant. They are especially numerous on the under side of rhizomes (Fig. 23 *w*), and also, when the external conditions are at all favourable, they seem to develop very readily from the stem nodes. A young shoot, or a cutting planted in moist soil, quickly forms adventitious roots, and roots may also arise in a similar manner from the bases of leaves, especially from *Begonia* leaves when planted in soil. The origin of adventitious roots, as of almost all roots, is endogenous. Dormant root rudiments occur in the same manner as dormant buds of shoots. Willow-twigs afford a special case of the presence of such dormant rudiments of adventitious roots, the further development of which is easily induced by darkness and moisture.

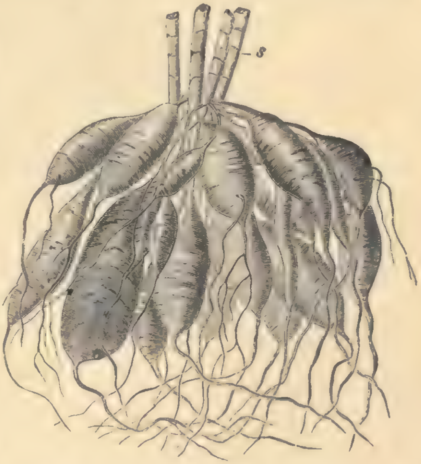


FIG. 51.—Root-tubers of *Dahlia variabilis*. *s*, The lower portions of the cut stems. ($\frac{1}{3}$ nat. size.)

When adventitious shoots are borne upon roots they mostly arise at some distance from the apex. In the Adder's Tongue Fern (*Ophioglossum*), the vegetative reproduction of which is effected by means of buds formed on the root, these arise close to the root-apex. Lastly, just as terminal leaves may arise from the apex of a stem and terminal shoots from the tips of the leaves of Ferns, in a few instances (species of *Asplenium* and *Platycerium*) a shoot may arise as the direct continuation of the growing point of a root (^{26}).

The Form of Subterranean Roots.—The customary nomenclature for the various root forms is based on their shape, size, and mode of branching. A root which is a prolongation downwards of the main stem is called the main root or TAP-ROOT; the other roots are termed, with reference to the tap-root, LATERAL ROOTS of different orders, according to the order of their development. A tap-root is present in Gymnosperms and many Dicotyledons, while it is, as a rule, wanting in Monocotyledons. The root system of most Monocotyledons and many Dicotyledons mainly consists of adventitious roots arising from the base of the stem or from underground stems or rhizomes. Roots which serve for storage of reserve materials may enlarge and become turnip-shaped or tuberous (Fig. 51). Such tuberous growths often greatly resemble stem tubers, but may be distinguished from them by their root-caps, by the absence of any indications of leaf development, and by their internal structure.

The morphology of the tubers of the Orchidaceae is peculiar. They are, to a great extent, made up of fleshy, swollen roots, fused together and terminating above in a shoot-bud. At their lower extremity the tubers are either simple or palmately segmented. In the adjoining figure (Fig. 52) both an old (*t′*) and a young tuber (*t″*) are represented still united together. The older tuber has produced its flowering shoot (*b*), and has begun to shrivel; a bud, formed at the base of the shoot, in the axil of a scale leaf (*s*), has already developed the adventitious roots, which, swollen and fused together, have given rise to the younger tuber. Roots of ordinary form arise from the base of the stem above the tuber.

Metamorphosis of Roots.—The aerial roots of tropical EPIPHYTES (27) differ considerably in their structure from underground roots. The aerial roots of the Orchidaceae and of many Aroideae are provided with a spongy sheath, the VELAMEN, by means of which they are enabled to absorb moisture from the atmosphere. Aerial roots, in some cases, grow straight downwards, and upon reaching the ground, branch and function as nutritive roots for the absorption of nourishment; in other instances, they turn from the light, and, remaining comparatively short and unbranched, fasten themselves as CLIMBING ROOTS to any support with which they come in contact. The climbing roots of many Orchids, Aroids, and Ferns branch and form lodgment places for humus; and into this absorbent branches of the climbing roots penetrate. Pendent aerial roots generally contain chlorophyll in their cortical tissue. In Orchids belonging to the genera *Angraecum* and *Taeniophyllum*, the task of nourishing the plant is left entirely to the aerial roots, which are then devoid of a velamen, and very much flattened. They are distinctly green-coloured, and supply the place of the leaves which lose their green colour and are reduced to scales. The flat, dorsiventral, chlorophyll-containing roots of the tropical Podostemaceae (28), which have been referred to with regard to the sequence of shoots (p. 29), fulfil a similar function. The aerial roots of the epiphytic Bromeliaceae are developed exclusively as climbing roots, while the leaves function not only as assimilating organs, but also assume the whole task of water-absorption. All the aerial roots of epiphytes are, so far as their origin is concerned, adventitious.

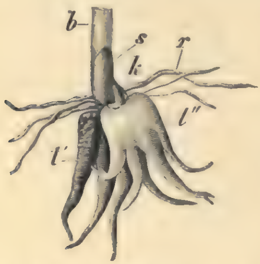


FIG. 52.—*Orchis latifolia.* *t′* The old root-tuber; *t″*, the young root-tuber; *b*, floral shoot; *s*, scale leaf with axillary bud, *k*, from which the new tuber has arisen; *r*, ordinary adventitious roots. (½ nat. size.)

The numerous adventitious roots which form a thickly matted covering on the trunks of Tree-ferns become hard after death, and serve as organs of protection.

In some Palms (*Acanthorrhiza*, *Iriartea*) the adventitious roots on the lower part of the stem become modified into thorns, ROOT-THORNS. The roots of certain tropical plants, such as *Pandanus* and the swamp-inhabiting Mangrove trees, are specially modified. These plants develop on their stems adventitious roots, which grow obliquely downwards into the ground, so that the stems finally appear as if standing on stilts. The Banyan trees of India (*Ficus indica*) produce wonderful root-supports from the under side of their branches, upon which they rest as upon columns. The lateral roots of certain Mangrove trees become modified as peculiar breathing organs, and for this purpose grow upwards into the air out of the swampy soil or water in which the trees grow, and are provided with special aerating passages. Such RESPIRATORY or AERATING ROOTS surround the Mangrove trees looking like vigorous Asparagus stalks, and enable the roots growing below in the mud to carry on the necessary exchange of gases with the atmosphere. (Cf. Fig. 213.)

Reduction of Roots.—There is a general relation between the degree of development of the leaf-surface and of the root-system. In saprophytic and parasitic plants, the shoots of which are as a rule extremely reduced, a corresponding reduction of the root-system can be recognised. Special absorbent organs or HAUSTORIA are often developed on the roots of parasites, *e.g.* on the roots of the green partial parasites *Euphrasia*, *Odontites*, *Thesium*, etc., which become attached to the roots of their host plants by means of disc-shaped or wart-shaped haustoria. In extreme cases no subterranean roots may be developed, and the parasite only bears haustoria which penetrate the host (*Cuscuta*, Fig. 202 *H*). The haustoria of the Rafflesiaceae traverse the body of the host-plant as elongated filaments of cells, and are capable of regenerating the parasite. The immense flowers of *Rafflesia Arnoldi*, which spring directly from the roots of *Cissus*, originate from similar haustoria. The reduction of the roots may extend to such a degree that, in a number of plants, no roots are formed. It has been already mentioned that in the case of *Coralliorrhiza innata* (Fig. 24) the rhizome assumes all the functions of the roots, which are entirely absent. Also in many aquatic plants (*Salvinia*, *Wolffia arrhiza*, *Utricularia*, *Ceratophyllum*) roots are altogether absent since these plants no longer require them. The beard-like epiphytic *Tillandsia usneoides*, belonging to the Bromeliaceae, has no roots and obtains the water it requires by means of special scale-like hairs.

Members of Independent Origin

The existence of parts of the plant with the characters of distinct primary members, but to which an independent phylogenetic origin must be ascribed, has been pointed out by GOEBEL ([29]). The tubers which occur among the Dioscoreaceae, an order of twining plants belonging to the Monocotyledons, are of this nature (Fig. 53). The extreme forms of these tubers are flat, cake-shaped bodies, which in development and structure exhibit a mixture of the characteristics of stem and root. The rhizophores of *Selaginella* (Fig. 54) which have been variously interpreted as leafless shoots, as roots, and as organs *sui generis*, also find their place here. They resemble leafless shoots, attain a considerable length, and may branch dichotomously and give rise to endogenous roots close to the growing points. As a matter of fact they are in structure and general behaviour intermediate between shoot and root, and it is not probable that they have originated from either of these primary members.

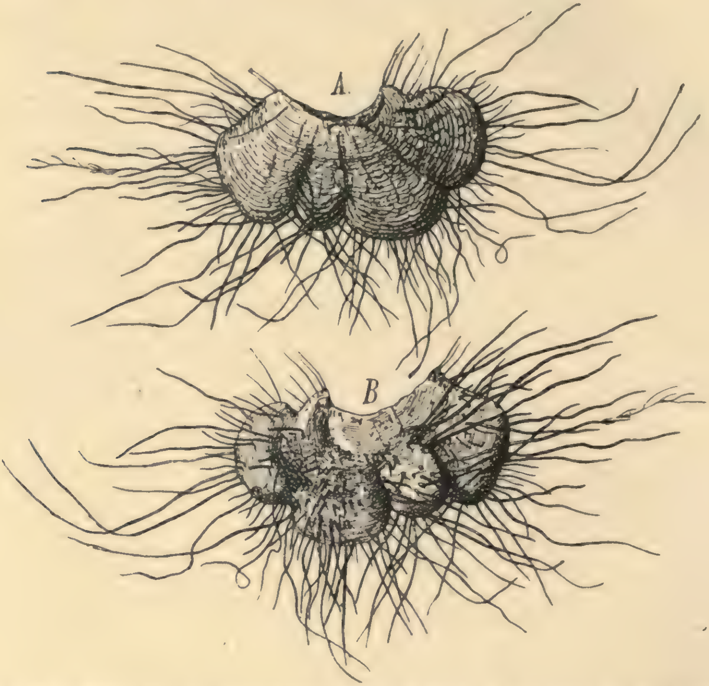


FIG. 53.—*Dioscorea sinuata.* Tuber separated from the shoot ; *A*, from above ; *B*, from below. The lower side bears roots. (After K. GOEBEL. ½ nat. size.)

Various outgrowths of the body of the plant to which an independent origin is to be ascribed are grouped together as EMERGENCES. A phylogenetic significance cannot be attached to the term as here used. It includes structures of the most different origin belonging both to the thallus and the cormus. The rhizoids, which serve to fasten the thallus of many Thallophytes and the cormus of the cormophytic Bryophyta to the substratum, as well as the massive attaching organs of many Brown Sea-weeds (Fucaceae and Laminariaceae) are classed here. So also are the structures which contain the asexual and sexual reproductive cells of the cryptogams (sporangia and sexual organs). In the sense of the term implied here the hairs, prickles, and glands borne on the surface of the highly organised plants must be included as well as the haustoria described above. As an extreme case the attaching organs (hapteræ) of the previously mentioned Podostemaceae may be referred to. These hapteræ serve to attach the nutritive roots of these plants firmly to the rocks exposed to rapidly flowing water, upon which they grow. They are at first conical outgrowths, but flatten out and become lobed when applied to the surface of the rock. The shoots originate from the flat nutritive roots. There is, indeed, no reason why outgrowths of the vegetative body of the plant should not become adapted to the performance of particular functions (30).

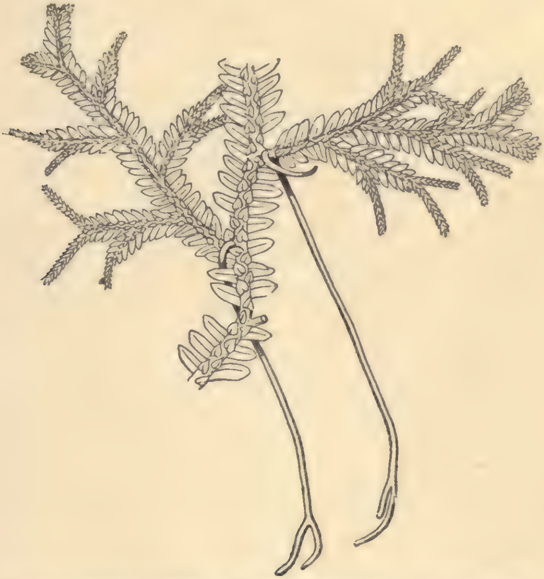


Fig. 54.—Part of the shoot of *Selaginella Martensii* with rhizophores. (From Goebel, *Organography*. Nat. size.)

MARINE BIOLOGICAL LIBRARY WOODS HOLE, MASS.

II. INTERNAL MORPHOLOGY

(Histology and Anatomy)

A. The Cell

1. STRUCTURE OF THE CELL

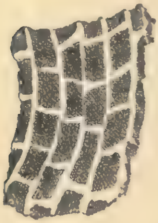


FIG. 55.—Copy of a part of HOOKE'S illustration of bottle-cork, which he described as "Schematism or texture of cork."

All plants and animals are composed of elementary organs called cells. In contrast to animal cells, typical vegetable cells are surrounded by firm walls, and are thus sharply marked off from one another. In fact, it was due to the investigation of the cell walls that the cell was first recognised in plants. An English micrographer, ROBERT HOOKE, was the first to notice vegetable cells. He gave them this name in his *Micrographia* in the year 1667, because of their resemblance to the cells of a honeycomb, and published an illustration of a piece of bottle-cork having the appearance shown in the adjoining figure (Fig. 55). ROBERT HOOKE, however, was only desirous of exhibiting by means of different objects the capabilities of his microscope; consequently, the Italian, MARCELLO MALPIGHI, and the Englishman, NEHEMIAH GREW, whose works appeared almost simultaneously a few years after HOOKE'S *Micrographia*, have been regarded as the founders of vegetable histology. The living contents of the cell, the real body or substance, was not recognised in its full significance until the middle of last century. Only then was attention turned more earnestly to this study, which has since been so especially advanced by MEYEN, SCHLEIDEN, HUGO V. MOHL, NÄGELI, DE BARY, FERDINAND COHN, PRINGSHEIM, and MAX SCHULTZE.

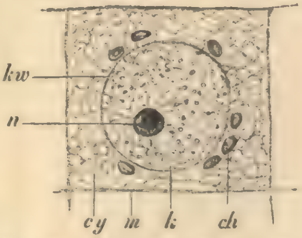


FIG. 56.—Embryonic cell from the vegetative cone of a phanerogamic plant. *k*. Nucleus; *kw*, nuclear membrane; *n*, nucleolus; *cy*, cytoplasm; *ch*, chromatophores; *m*, cell wall. (Somewhat diagrammatic, × circa 1000.)

If an examination be made of a thin longitudinal section of the apex of a stem of a phanerogamic plant, with a higher magnifying power than that used in the previous investigation (Fig. 17) of the vegetative cone, it will be seen that it consists of nearly rectangular cells (Fig. 56), which are full of protoplasm and separated from one another by delicate walls. In each of the cells there will be clearly distinguishable a round body (*k*), which fills up the greater part of the cell cavity. This body is the cell NUCLEUS. If sections, made in different directions through the vegetative cone, be compared with one another, it will be seen that its component cells are nearly cubical or tabular, while the nuclei are more or less spherical or disc-shaped. The finely granular substance (*cy*) filling in the space between the nucleus (*k*) and the cell wall (*m*) is the CELL PLASM or CYTOPLASM. In the cytoplasm there are to be found, about the nucleus, a number of colourless and highly refractive bodies: these are the pigment-bearers or CHROMATOPHORES (*ch*). NUCLEUS, CYTOPLASM, AND CHROMATOPHORES, CONSTITUTE THE ELEMENTS OF THE LIVING BODY OF A TYPICAL VEGETABLE CELL. To designate all these collectively, it is customary to use the term PROTOPLASM, which is then to be understood as including all the living constituents of the cell or PROTOPLAST.

In many animal cells modern investigations have revealed, in addition to the constituents of the protoplasm just mentioned, a small structure situated close to the nucleus, which has been termed the CENTROSOME, CENTRIOLE, or ATTRACTION-SPHERE. Similar structures have been demonstrated in the lower cryptogamic plants (Fig. 57 *c*), but they appear to be wanting in the cells of the higher Cryptogams and the Phanerogams (31).

The nucleus and cytoplasm are the two most essential constituents of the cell, and its vital functions depend on the interaction between them. In the lowest plants (Cyanophyceae and Bacteria) such a division of labour in the protoplasm is not certainly proved, the existence of a nucleus being still a matter of dispute (32). Chromatophores are wanting in the Bacteria and Fungi, as in all animal cells.

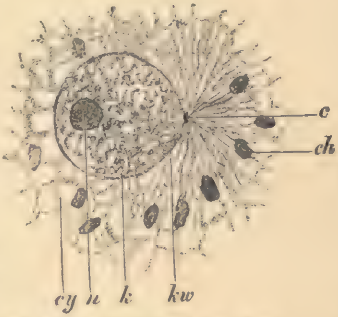


FIG. 57.—A nucleus of a cell of the young plant of *Fucus serratus*, a Brown Seaweed. *cy*, The surrounding cytoplasm; *k*, the nucleus; *kw*, nuclear membrane; *n*, nucleolus; *c*, centrosome; *ch*, chromatophores. (× 1000.)

While animal cells usually remain continuously filled with protoplasm, vegetable cells soon form large SAP CAVITIES. It is only the embryonic cells of plants that are entirely filled with protoplasm, as the cells, for example, of an embryo or of a growing point; they afterwards become larger and contain proportionally less protoplasm. This can be seen in any longitudinal section through a stem apex. At a short distance from the growing point the enlarged cells have already begun to show cavities or VACUOLES (*v* in *A*, Fig. 58) in their cytoplasm. These are filled with a watery fluid, the CELL SAP. The cells continue to increase in size, and usually soon attain a condition in which their whole central portion is filled by a single, large sap cavity (*v* in *B*, Fig. 58). The cytoplasm then forms only a thin layer lining the cell wall, while the nucleus takes a parietal position in the peripheral cytoplasmic layer. At other times, however, the sap cavity of a fully-developed cell may be traversed by bands and threads of cytoplasm; and in that case the nucleus is suspended in the centre of the cell. But whatever position the nucleus may occupy, it is always embedded in cytoplasm; and there is always a continuous peripheral layer of cytoplasm lining the cell wall. This cytoplasmic peripheral layer is in contact with the cell wall at all points, and, so long as the cell remains living, it continues in that condition. In old cells, however, it frequently becomes so thin as to escape direct observation, and is not perceptible until some dehydrating reagent, which causes it to recede from the wall, has been employed. Such a thin cytoplasmic peripheral layer has been described by Hugo v. Mohl under the name of PRIMORDIAL UTRICLE.

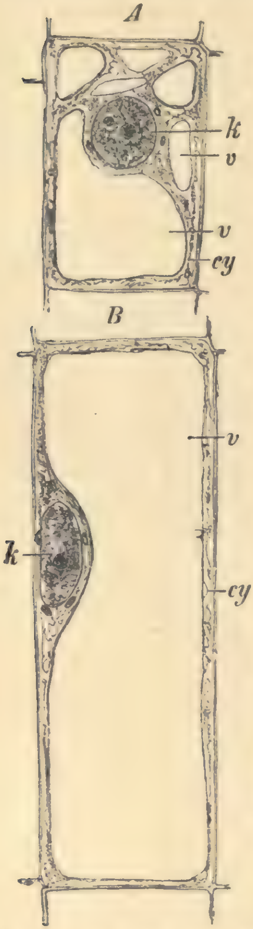


Fig. 58.—Two cells taken at different distances from the growing point of a phanerogamic shoot. *k*, Nucleus; *cy*, cytoplasm; *v*, vacuoles, represented in *B* by the sap cavity. (Somewhat diagrammatic. × circa 500.)

Dead cells lose their living protoplasmic contents, and, strictly speaking, should no longer be termed cells, although the name was first applied to them when in that condition. In reality they represent only cell cavities. With their death, however, cells do not lose their importance to a plant. Without such cell cavities a highly-organised plant could not exist, as they perform for it the office of water-carriers, and afford mechanical support and rigidity. The heart wood of a tree consists exclusively of the walls of dead cells.

The Protoplasm.—In order to facilitate an insight into the real character of protoplasm, attention will first be directed to the Slime Fungi (Myxomycetes), a group of organisms which stand on the border between the animal and vegetable kingdoms. These Myxomycetes are characterised at one stage of their development by the formation of a PLASMODIUM, a large naked mass of protoplasm.

The plasmodium is formed from the protoplasm of the spores. These spores are unicellular bodies (Fig. 59 *a*, *b*), filled with cytoplasm, in which lies a central nucleus, and are surrounded by resistent cell walls. The spores germinate in water, their contents, breaking through the spore walls, come out (*c*, *d*) and round themselves off. A change of form soon takes place; the protoplasmic mass elongates and assumes somewhat the shape of a pear, with the forward end prolonged into a fine whip-like process or flagellum (*e*, *f*, *g*). Thus the contents of the spore have become transformed into a SWARM-SPORE, which now swims away by means of whip-like movements of its flagellum. In addition to the nucleus, which is visible in the anterior end of every swarm-spore, a vesicle may be seen at the other end, which, after gradually increasing in size, suddenly vanishes, only to swell again into view. This

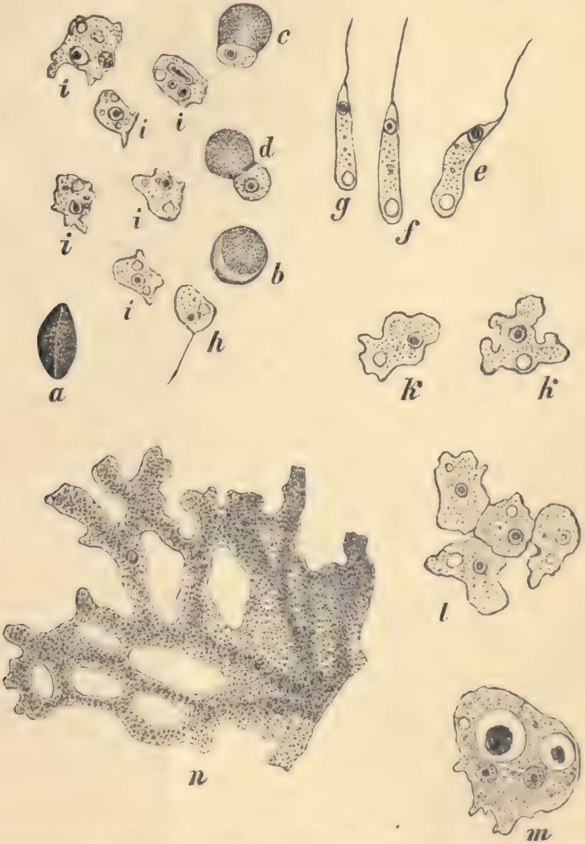


FIG. 59.—*Chondrioderma difforme*. *a*, Dry, shrivelled spore; *b*, swollen spore; *c* and *d*, spores showing escaping contents; *e*, *f*, *g*, swarm-spores; *h*, swarm-spore changing to a myxoamoeba; *i*, younger, *k*, older myxoamoeba; *l*, myxoamoebae about to fuse; *m*, small plasmodium; *n*, portion of fully-developed plasmodium. (*a*-*m*, × 540: *n*, × 90.)

vesicle is a CONTRACTILE VACUOLE. The presence of such a contractile vacuole in an organism was formerly considered a certain indication of its animal nature. Now, however, contractile vacuoles have been observed in the swarm-spores of many green Algae, of whose vegetable nature there can be no doubt.

The swarm-spores of the Myxomycetes soon lose this characteristic swarm-movement, draw in their flagella, and pass into the amoeba stage of their development, in which, like animal amoebae, they assume irregular, constantly changing shapes, and are capable of performing only amoeboid creeping movements. In the case of *Chondrioderma difforme*, a Myxomycete of frequent occurrence in rotting parts of plants (Fig. 59), a number of the amoebae eventually collect together (*l*) and coalesce. In this way, as is also the case with most other Myxomycetes, the amoebae ultimately give rise to a plasmodium (*n*).

Although each one of the amoebae is so small that it can only be seen with the aid of a microscope, the plasmodium into which they become united may attain a considerable size.

The cytoplasm, both of the single amoeba and of the plasmodium, consists of a clear ground substance, through which granules are distributed. This substance is of the consistence of a tenacious fluid; its superficial region is denser and free from granules, while these are numerous in the less dense central portion. The granules enable the internal streaming movements of the cytoplasm to be recognised. The currents are constantly changing their direction, moving either towards or away from the margin. The formation and withdrawal of processes of the margin stand in relation to the direction of the currents. When naked masses of protoplasm such as these plasmodia encounter foreign bodies, they can enclose them in vacuoles, and, when of use as food, digest them.

Deprived of its component water the protoplasm becomes hard and tenacious, and, without losing its vitality, ceases to perform any of its vital functions until again awakened into activity by a fresh supply of water. In case of a scarcity of water the plasmodia of the Myxomycetes may form SCLEROTIA, that is, masses of resting protoplasm of an almost wax-like consistency. Months and indeed sometimes years afterwards, it is possible for such sclerotia, if water be supplied, to again produce motile plasmodia. Similarly, in seeds kept for a long time, the protoplasm consolidates into a hard mass, which may be easily cut with a knife, while the nuclei will be found to have shrunk and lost their original shape. Nevertheless the protoplasts, after absorbing water, may return again to a condition of activity.

Protoplasm is not a simple substance chemically; it consists rather of numerous different components, which are subject to continual change. Since albuminous substances are always present, protoplasm always gives a proteid reaction; when incinerated, fumes of ammonia are given off.

Active protoplasm generally gives an alkaline, and, under certain conditions, a neutral reaction, but never an acid one. The protoplasm of the higher plants coagulates at a temperature not much over 50° C., in the Schizophyta, however, usually not below 75° C. In the inactive dried condition, as in spores and seeds, it can endure a still higher temperature without coagulating. The spores of many Bacteria can withstand a temperature as high as 105° C. Treated with alcohol or ether, with acids of definite concentrations, with bichromates of the alkali metals, or with corrosive sublimate, protoplasm quickly coagulates, while at the same time insoluble proteid compounds are formed. Coagulating reagents, accordingly, play an important part in microscopic technique; of especial value are those, which, while fixing and hardening the protoplasm, change its structure in the least degree. As fixing and hardening reagents for vegetable tissues, alcohol, 1 per cent chromic acid, 1 per cent acetic acid, 0·5 to 1 per cent osmic acid, concentrated picric acid, or corresponding mixtures of these acids, solutions of mercuric chloride and formaldehyde, are used. Iodine stains protoplasm brownish yellow; nitric acid, followed by caustic potash, yellowish brown (xanthoprotein reaction); sulphuric acid, if sugar be present, rose red. Acid nitrate of mercury (MILLON's reagent) gives to protoplasm a brick-red colour. These reactions occur with all proteid substances though they are not absolutely distinctive of them. Protoplasm is soluble in dilute caustic potash and also in eau de Javelle (potassium-hypochlorite), and accordingly both of these reagents may be recommended for clearing specimens, when the cell contents are not to be investigated. All of the above-mentioned reagents kill protoplasm; until they have done so, their characteristic reactions are not manifested.. A large number of albuminous bodies or albuminates have been named which are said to enter into the composition of living protoplasm. Most of these compounds are still ill-defined; in nuclei the nucleins are most important, but they are also found in the cytoplasm. They are characterised by containing much phosphorus, and are not attacked by pepsin, and only with difficulty by trypsin. Staining reagents have also become an important help to microscopic investigations for determining the composition of protoplasm. This is due to the fact that the different constituents of protoplasm take up and retain the stain with different degrees of intensity and energy. As a general rule, only coagulated protoplasm can absorb colouring matter, although some few aniline stains can, to a limited extent, permeate living protoplasts. For staining vegetable protoplasts, which have been previously fixed, the various carmines, hæmatoxylin, safranin, iodine green, acid fuchsin, eosin, methylene blue, and aniline blue, gentian-violet and orange, have been found particularly convenient. The different components of the protoplasm absorb the stains with different intensities, and, when reagents are employed to remove the colouring matters, they exhibit differences in their power to retain them. The nucleus generally becomes more intensely coloured than the rest of the protoplasm, especially a part of its substance, which is therefore called CHROMATIN. In addition to those substances, which are to be regarded as integral parts of active protoplasm, it always includes derivative products of albuminates, particularly amides, such as asparagin, glutamin; also ferments, such as diastase, pepsin, invertin; at times alkaloids, and always carbohydrates and fats. The ash left after incineration also shows that protoplasm always contains mineral matter, even if only in small quantities. All such substances which do not enter directly into the composition of protoplasm, but are only included within it, are designated by the term METAPLASM.

The Cytoplasm.—The cytoplasm of vegetable cells, which possess a cell wall, is a more or less tenacious fluid. It partakes of the physical properties of fluids, and on being artificially freed from the cell wall, tends to assume the spherical form. Its cohesion appears to be greater in meristematic cells than in those which are older, while in certain cases a still firmer consistence may be attained as in the cilia borne by swarm-spores.

Both in the case of the Myxomycete and of the vegetable cell enclosed by a wall, the basis of the cytoplasm consists of a hyaline substance termed the HYALOPLASM. When granules are distributed through the cytoplasm it is spoken of as GRANULAR PLASMA or polioplasm. An extremely thin boundary layer is found at the periphery which is quite free from granules, and a similar layer bounds every vacuole present in the cytoplasm. The wall of the vacuole is characterised by a greater tenacity of life than the rest of the cytoplasm, remaining alive for some time after the latter has been killed by the action of a 10 per cent solution of potassium nitrate. Since the vacuole wall regulates the pressure exerted by the cell sap contained in the vacuole, HUGO DE VRIES has applied the name TONOPLAST (33) to this layer.

The small granules distributed through the granular plasma consist of various substances, and may be classed together as MICROSOMES. Some of them are small cavities filled with dissolved substances, and to these the name PHYSODES has been given.

Even though bounded by a cell wall the cytoplasm frequently exhibits movements comparable to those of the naked amoebae and plasmodia of Myxomycetes. These movements mostly are found in somewhat old cells, but N. GAIDUKOV (34) has shown by means of the recently invented ultramicroscope that they are of widespread occurrence in vegetable protoplasts. The study of the movements in the Myxomycetes showed that various kinds of movements could be distinguished; the waving movement of the flagellum of the swarm-spore, the change in external form of amoebae and plasmodia, to which their power of creeping about is due, and finally a streaming movement in the cytoplasm. The cytoplasm, enclosed by a cell-wall, may either exhibit isolated streaming movements, the direction of which may undergo reversals, or a single stream, the direction of which is constant. These two forms of movement are distinguished as CIRCULATION and ROTATION respectively. In rotation, which is found in cells with the cytoplasm reduced to a layer lining the wall, the single continuous current follows the cell wall. In circulation, on the other hand, the layer of cytoplasm lining the wall takes no part in the movement, which is found in the strands traversing the vacuole. Circulation is common in cells of land-plants, while rotation is more usual in water-plants. The stimulus caused by wounding the tissues in making the preparation frequently increases the activity of the movement (35).

A particularly favourable object for the study of protoplasm in circulation is afforded by the staminal hairs of *Tradescantia virginica*. In each cell (Fig. 60) small, fine currents of protoplasm flow in different directions in the peripheral cytoplasmic layer, as well as in the cytoplasmic threads, which penetrate the sap cavity. These cytoplasmic threads gradually change their form and structure, and thus alter the position of the cell nucleus.

When the protoplasm is in rotation, the cell nucleus and chromatophores are usually carried along by the current, but the chromatophores may remain in the boundary layer, and thus not undergo movement. This is the case with the Stoneworts (Characeae), whose long internodal cells, especially in the genus *Nitella*, afford good examples of well-marked rotation.

Properly fixed cytoplasm has a finely reticulate or honeycomb-like structure, small granules being embedded in the network. At particular developmental stages this structure appears to be traversed by special filaments, which can be demonstrated by suitable staining (Fig. 57) (36).

The portion of the cytoplasm which forms the network or honeycomb appears to be specially concerned with the nutritive processes, while the fibrillar plasma influences the process of development; they are respectively termed trophoplasm and kinoplasm; the latter has also been called archeplasm. When traced to their origins the limiting layer of the cytoplast is found to belong to the kinoplasm, the walls of vacuoles to the trophoplasm. Albuminous substances, precipitated by the fixing agent, have not infrequently been mistaken for structural features of the cytoplasm (37).

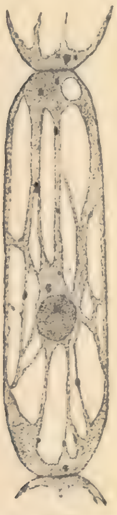


FIG. 60.—Cell from a staminal hair of *Tradescantia virginica*, showing the nucleus suspended by protoplasmic strands. (× 240.)

The Cell Nucleus (38).—The resting nucleus has a reticulate or honeycomb structure forming an anastomosing network (Fig. 56), which, however, in living objects can only be distinguished by the punctated appearance it gives to the nucleus. Streaming movements do not take place within the nucleus. An insight into the nuclear structure is only to be attained with the help of properly fixed and stained preparations. It is then possible to determine that the greater part of this nuclear network is composed of delicate and, for the most part, unstained threads, in which lie deeply stained granules. The substance of the threads has been distinguished as LININ (*l*), that of the granules as CHROMATIN (*ch*). One or more larger bodies, the NUCLEOLI (*n*), occur at the intersections of some of the linin threads; these, although deeply stained, do not take the same tint as the chromatin granules. The network of the nucleus lies within the nuclear cavity, which is filled with nuclear sap and surrounded by a membrane (*w*). The nuclear membrane, strictly speaking, is a part of the surrounding cytoplasm, and is the protoplasmic layer with which the cytoplasm separates itself from the nuclear cavity. The nucleus in young cells with abundant protoplasm is, as a rule, spherical. When situated in the lining layer of cytoplasm of older cells, it is frequently of a flattened form, while in elongated cells it exhibits a corresponding elongation. Exceptionally in old cells the nucleus is forked, lobed, or of some other irregular shape. These changes in form of the nucleus are due to slow movements, which cannot, as a rule, be directly observed. In embryonic tissues the nuclei are relatively large in proportion to the size of the protoplasts. Glandular cells are also usually provided with large nuclei.

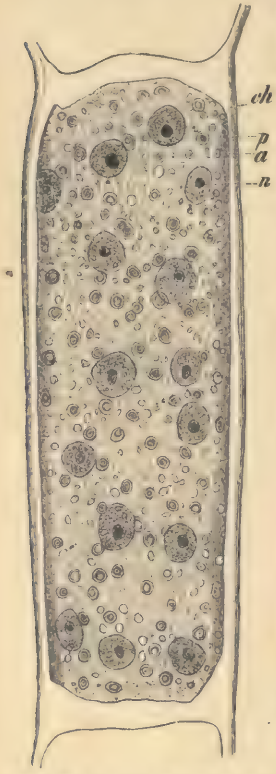


Fig. 61.—A cell of *Cladophora glomerata*, fixed with 1 per cent chromic acid and stained with carmine. *n*, Nuclei; *ch*, chromatophores; *p*, pyrenoids; *a*, starch grains. (× 540.)

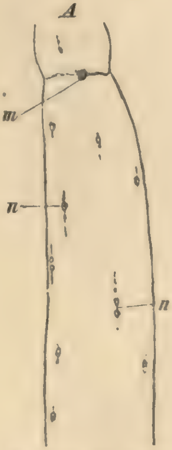


Fig. 62.—Portions of two adjacent cells in a hypha from the stalk of *Psalliota arvensis*. *n*, Nuclei; *m*, pits. (× 540.)

While the cells of the Cormophytes are almost always uninucleate, in the Thallophytes, on the contrary, multinucleate cells are by no means infrequent. In the Fungi, and in the Siphoneae among the Algæ, they are the rule. The whole plant is then composed either of but one single multinuclear cell, which may be extensively branched (Fig. 295), or it may consist of a large number of multinuclear cells, forming together one organism. Thus, on suitable treatment, several nuclei may be detected in the peripheral cytoplasm of each of the cells of the common filamentous fresh-water Alga *Cladophora glomerata* (Fig. 6, p. 12, Fig. 61).

The nuclei of the long, multinucleate cells (Fig. 62 *n*) of fungal filaments, or HYPHÆ, and also of many Siphoneae, are characterised by their diminutive size.

The Centrioles and Centrosomes.—In a number of cases among the lower Cryptogams (Thallophyta and Bryophyta) structures which correspond to the centrioles and centrosomes of animal cells have been demonstrated. Where centrioles are found, as in some marine Algae (*Fucus*, Fig. 57), they are dumb-bell shaped. Larger masses of active cytoplasm occur in a number of Fungi, and, though they do not, like them, include centrioles, are comparable with the centrosomes of animal cells. Similar structures occur in the mother-cells of the spermatozoids in Bryophyta, Pteridophyta, and certain Gymnosperms (39). They are there termed blepharoplasts, and provide the material for the formation of the cilia of the spermatozoids. With the exception of the blepharoplasts no structures comparable with centrioles or centrosomes have been shown to exist in the cells of the higher plants.

The Chromatophores (40).—In the embryonic cells of the embryo and of growing points, where the chromatophores (Fig. 56 *ch*) are principally located around the nucleus, they first appear as small, colourless, highly refractive bodies. They may retain the same appearance in older cells (Fig. 111 *A*, *l*), but in them they also attain a further development, as CHLOROPLASTS, LEUCOPLASTS, or CHROMOPLASTS. Since these bodies have the same origin they are all included in the one term, CHROMATOPHORES.

Chloroplasts.—In parts of plants which are exposed to the light the chromatophores usually develop into chlorophyll bodies or chloroplasts. These are generally green granules of a somewhat flattened ellipsoidal shape (Fig. 63), and are scattered, in numbers, in the parietal cytoplasm of the cells. All the chloroplasts in the Cormophytes, and, for the most part also, in the green Thallophytes, have this form. In the lower Algae, however, the chlorophyll bodies may assume a band-like (Fig. 264 *c*), stellate or tabular shape.

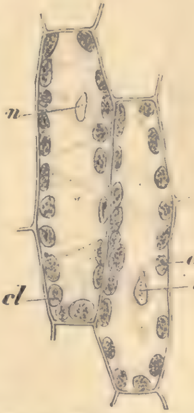


FIG. 63.—Two cells from a leaf of *Funaria hygrometrica*. *cl*, Chloroplasts; *n*, nucleus. (× 300.)

In these cases the chloroplast often includes one or more pyrenoids; these are spherical protoplasmic bodies containing an albuminous crystalloid, and are surrounded by small grains of starch (Fig. 264). The ground substance of the chlorophyll bodies is itself colourless, but contains numerous coloured granules, which are termed GRANA. These consist of an oleaginous substance, which holds in solution green and yellow pigments. These colouring substances may be extracted by means of alcohol, leaving only the colourless plasmic substance of the chlorophyll body remaining.

The easiest way in which a solution of chlorophyll can be prepared, is to extract the chlorophyll by means of alcohol from green leaves that have been previously boiled in water. The green chlorophyll pigment is also soluble in ether, fatty and ethereal oils, paraffin, petroleum, and carbon disulphide. The alcoholic solutions are fluorescent and appear green in transmitted light, blood red in reflected light. When an alcoholic solution of chlorophyll is shaken up with benzole, the latter, as KRAUS first showed, on standing rises to the surface as a green solution, leaving the alcohol yellow.

According to MARCHLEWSKI and SCHUNCK (41), two green pigments are to be detected in the alcoholic extract from leaves. The one, true chlorophyll, is always present; the other, which has been termed allochlorophyll, cannot be detected in some plants. The yellow pigments of the chloroplasts are collectively termed xanthophyll. Only chrysophyll, which forms shining red crystals, has been isolated; the rest of the xanthophyll form amorphous masses. True chlorophyll is characterised by three absorption bands in the less refrangible half of the spectrum, and three in the more refrangible portion. As yet only one band, which lies in the red portion of the spectrum, is known for allochlorophyll. The amount of chlorophyll in a green plant is very small. TSCHIRCH (42) has calculated that only 0·2–1·0 gr. of chlorophyll can be obtained from a square metre of green foliage leaves.

From the investigations of MARCHLEWSKI and NENCKI it appears that a relationship exists between chlorophyll and hæmoglobin (the pigment contained in red blood corpuscles) (43).

The green colour of the chlorophyll in some groups of Algae is more or less masked by other pigments. In addition to the chlorophyll green, with its accompanying yellow pigments, many of the blue-green Schizophyceae contain a blue colouring matter, phycocyanin, while the red Algae possess a red pigment termed phycoerythrin. These pigments are soluble in water, and are characterised by a beautiful fluorescence. The phycocyanin may often be found as a blue border surrounding a blue-green Fission-Alga which has been dried in a press.

Whether these pigments are mixed with the chlorophyll or are chemically combined with it is as yet undecided (44). Recently HANS MOLISCH (45) has attempted to prove that the brown coloration of the Diatoms, the brown Algae, and especially of a saprophytic Orchid (*Neottia nidus avis*), is not due to a mixture of a brown pigment with chlorophyll. He regards it as due on the other hand to a single pigment, phæophyll, which is nearly related to chlorophyll and readily undergoes a chemical change into ordinary chlorophyll.

Before the leaves of trees fall in the autumn their cells lose nearly all their cytoplasmic contents, and at the same time the chloroplasts undergo disorganisation. There remains only a watery substance in the cell cavity, in which a few oil globules and crystals, together with a few yellow, strongly refractive bodies, can be seen. Sometimes in presence of abundant sugar this liquid in the cell cavities becomes red, and thus imparts to the foliage its autumnal brilliancy. In the leaves of coniferous trees, which only indicate the approaching winter by assuming a somewhat brownish tint, the cause is different. The chlorophyll-green of their chloroplasts changes to a brownish green pigment, but in the following spring regains its characteristic colour.

In such phanerogamic parasites or humus-plants as are devoid of green colour, the chloroplasts either do not develop, or they are white, or have only a brownish or reddish colour. No chromatophores are found in the Fungi.

Leucoplasts. — In the interior of plants, where light cannot penetrate, leucoplasts are developed from the rudiments of the chromatophores instead of chloroplasts. They are of a denser consistency than the chloroplasts, mostly spherical in shape, but often somewhat elongated in consequence of enclosed albuminous crystals. If the leucoplasts become at any time exposed to the light, they may change into chloroplasts. This frequently occurs, for example, in the superficial portions of potato tubers.

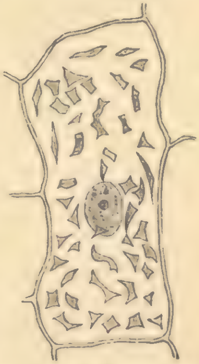


FIG. 64.—Cell from the upper surface of the calyx of *Tropaeolum majus*, showing chromoplasts. (× 540.)

Chromoplasts.—The chromoplasts of most flowers and fruits arise either directly from the rudiments of colourless chromatophores, or from previously formed chloroplasts. In shape the chromoplasts resemble the chloroplasts, except that they are usually smaller; in consequence of the crystallisation of their colouring pigment they sometimes assume a triangular, tabular, needle, or fan-shaped form (Figs. 64, 65). The colour of the chromoplasts varies from yellow to red, according to the predominance of yellow xanthophyll or orange-red carotin. The name carotin has been derived from the Carrot (*Daucus Carota*), in the roots of which it is particularly abundant (Fig. 65). The frequent crystalline form of the chromoplasts is, in a great part, due to the tendency of carotin to crystallisation, although it may be also occasioned by needle-like crystals of albumin. Xanthophyll, however, is never present in the chromoplasts except in an amorphous condition.

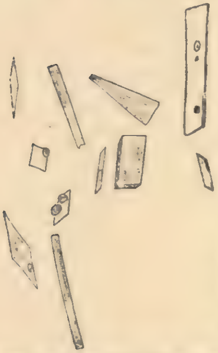


FIG. 65.—Chromoplasts of the Carrot, some with included starch grains. (× 540.)

Carotin is practically identical with the chrysophyll found in the chloroplasts. Its spectrum only differs from that of chrysophyll in having the absorption bands slightly displaced towards the violet end ([46]).

Origin and Structure of the Cell Wall ([47]).—The membrane which encloses the vegetable protoplast is a product of the protoplasm. Many low organisms belonging to the Algae liberate naked protoplasts from their cells; these swarm-spores (Fig. 97 *A*) serve to multiply the plant vegetatively. They soon settle down, form a thin cell membrane on the surface of the protoplast, and proceed to give rise to a filament. In more highly organised plants the ovum, from which the development starts, has no cell wall until it has been fertilised; from this stage on, all the cells composing the plant are surrounded by cell walls. At the growing points of plants the cells are separated from one another only by extremely thin membranes or cell walls. As the cells increase in number by repeated division, new cell walls are being continually introduced between the existing ones. The rapid growth in length which sets in a short distance from the growing point, as a result of the increase in the size of the cells, must be accompanied by a corresponding GROWTH IN SURFACE of the cell walls. So long as this growth in surface continues, the cell walls remain thin. After the cells have attained their ultimate size, the GROWTH IN THICKNESS of the cell walls then begins. The growth in surface of the cell wall may either involve the introduction of new material, or may take place without this. In the latter case the membrane would become thinner if new lamellae were not simultaneously applied to its surface. Growth of the wall by the introduction of new particles between those previously existing is termed GROWTH BY INTUSSUSCEPTION, while that which occurs by the laying down of new lamellae on the surface of the older ones is called GROWTH BY APPOSI-

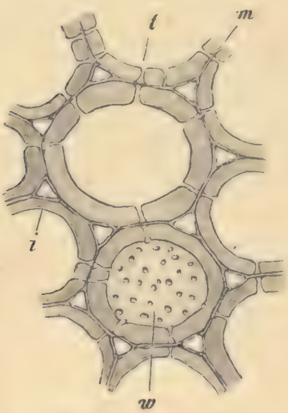


FIG. 66.—Strongly thickened cell from the pith of *Clematis vitalba*. *m*, Middle lamella; *i*, intercellular space; *t*, pit; *w*, pitted} cell wall in surface view. (× 300.)

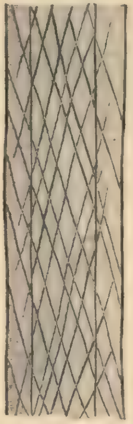


FIG. 67.—Part of a sclerenchymatous fibre from *Vinca major*. The striations of the outer layers are more apparent than those of the inner layers. The thickness of the wall, as seen in optical section, is also shown. (×500.)

TION. The later growth in thickness of most cell walls takes place by apposition, and thus the stratification, which such thickened walls exhibit, is brought about (Fig. 66). Thicker, dense layers alternate with thinner less dense ones. The denser layers can be recognised by their high refractive power. In many cases lamellæ, deposited by apposition, become further thickened and otherwise modified by a process of intussusception. Three distinct layers can frequently be distinguished in strongly thickened cell walls, such as those of the wood, a primary, a secondary, and a tertiary thickening layer; these differ in their optical appearance and their chemical composition. The secondary thickening layer is usually the most strongly developed, and forms the chief part of the cell wall. The tertiary or inner layer is usually more highly refractive.

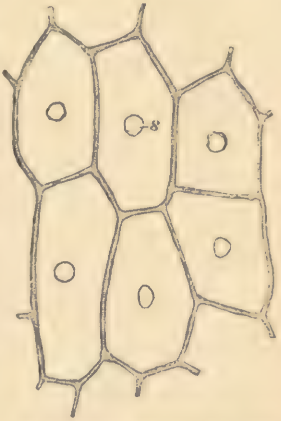


FIG. 68.—Surface view of cells from the sensitive side of the tendril of *Cucurbita Pepo*, showing tactile pits, *s*. (× 540.)

Thicker cell walls or layers of the wall which appear homogeneous frequently exhibit a stratification when treated with strong acids or alkalies. In many cases the thickening layers exhibit delicate striations in surface view. The striations extend through the whole thickness of the layers, usually running obliquely to the long axis of the cell, and often crossing one another in the different thickening layers (Fig. 67). A similar appearance of crossing of striations may result from the single thickening layers of two adjoining cells being visible at once. In special cases, but only in the formation of reproductive cells, an inner thickening layer, completely detached from the others, is produced, as in the formation of pollen grains and the spores of Bryophytes and Pteridophytes, which, enclosed only by this inner membrance, finally become freed from the older thickening layer. This process is often alluded to as REJUVENESCENCE; in such cases, it should be noted, there are, in reality, no new cells formed.

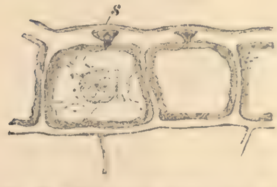


FIG. 69.—Transverse section through similar cells to those in Fig. 68; a small crystal of calcium oxalate is present in the tactile pits. (×450.)

The thickening of the cell wall seldom takes place uniformly over the whole surface; but some portions are thickened, while, at other points, the original cell wall remains thin. In this way pores are formed which penetrate the thickening layers. These pores or PITS may be either circular (Figs. 66 *w*, 71 *m*), elliptical, or elongated. The pits in adjoining cells coincide, and would form one continuous canal, were it not that the unthickened primary cell wall persists as a PIT MEMBRANE between the two pits. The openings of narrow elliptical pits into adjoining cells usually appear to cross one another obliquely. As a result of the continued thickening of the cell wall, the canals of several pits often unite, and so BRANCHED PITS are formed. Such branched pits have usually very narrow canals, and occur for the most part only in extremely thick and hard cell walls, as, for instance, in those of the so-called sclerotic cells or

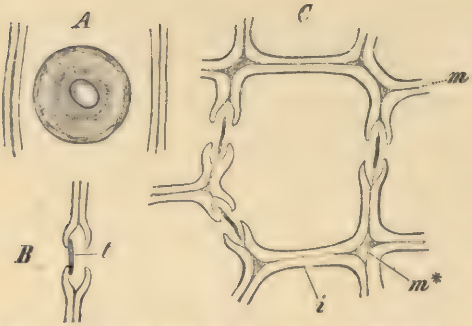


FIG. 70.—From the wood of the Pine, *Pinus sylvestris*. *A*, **Bordered pit in surface view; *B*, bordered pit in tangential section; *t*, torus; *C*, transverse section of a tracheid; *m*, middle lamella, with gusset, *m****; *i*, inner peripheral layer. (× 540.)

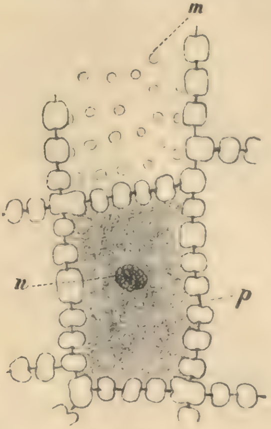


FIG. 71.—Cells from the endosperm of *Ornithogalum umbellatum*. *m*, Pits in surface view; *p*, closing membrane; *n*, nucleus. (× 240.)

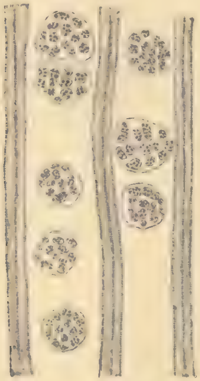


FIG. 72.—Part of two sieve-tubes of the Pine, *Pinus sylvestris*, showing sieve-pits. (× 540.)

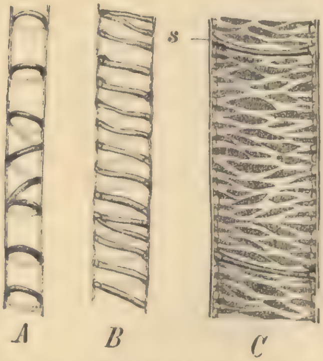


FIG. 73.—*A*, Part of an annular tracheid; *B*, part of a spiral tracheid; *C*, longitudinal section through part of a reticulate vessel, showing the remains of a partition wall, *s*. (× 240.)

sclereides. Simple pits may, on the other hand, expand on approaching the primary cell wall.

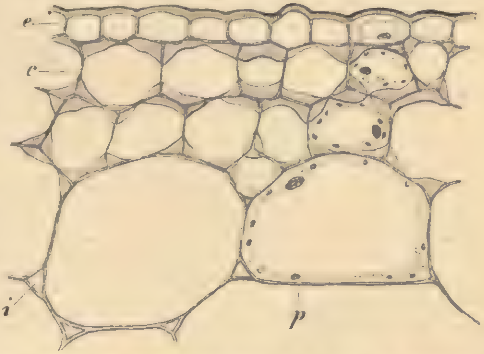


FIG. 74.—Part of transverse section of a stem of *Impatiens parviflora*. *e*. Epidermis; *c*, collenchyma; *p*, thin-walled parenchymatous cells; *i*, intercellular space. (× 300.)

Pits widened towards the membrane are found in the external cell walls of many tendrils (48). These pits, which are filled with cytoplasm, probably receive the stimulus, and may be termed tactile pits (Figs. 68, 69). The structures known as BORDERED PITS (Fig. 70) are a special type of simple pits widened towards the pit membrane. The pit may be present on one or both sides of the wall; the former is the case when the water-conducting element abuts on a cell with protoplasmic contents, the latter when the pitted wall separates two water-conducting elements. In bordered pits the closing membrane is thickened at the centre to form a TORUS (Fig. 70, *B*). By the curving of the closing membrane to one side or the other the torus may so act as to close the pit canal (Fig, 70 *B*, *t*). The bordered pits apparently act as valves. Seen from the surface a bordered pit appears as two concentric rings (Fig. 70 *A*). The smaller, inner ring represents the narrow opening of the pit into the cell cavity; the larger, outer ring indicates the widest portion of the PIT CHAMBER when it abuts on the primary cell wall.

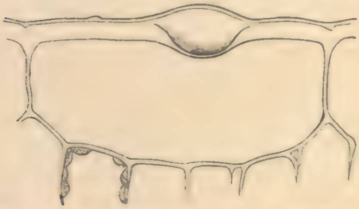


FIG. 75.—Epidermal cell from the margin of a radical leaf of *Campanula persicifolia*. The lens-shaped thickening of the outer wall is in this plant silicified. (After HABERLANDT, × 515.)

The pit membrane of specially wide pits between cells with thin walls often shows thicker bands which give it a lattice-work appearance. A similar type of thickening is found in the membranes of the sieve-pits which, on account of their being perforated like a sieve, are termed sieve-plates (Fig. 72).

In cases where the greater part of the cell wall remains unthickened, its character is determined by its thickened rather than by its unthickened portions; it is in this sense that the terms annular, spiral, and reticulate are used (Fig. 73). Just as in the case of cells with bordered pits, annular, spiral, and reticulate cell walls are only acquired by cells that soon lose their contents, and act as water-carriers. Such wall thickenings serve as mechanical supports, to give rigidity to the cells, and to enable the cell walls to withstand the pressure of the surrounding living cells.

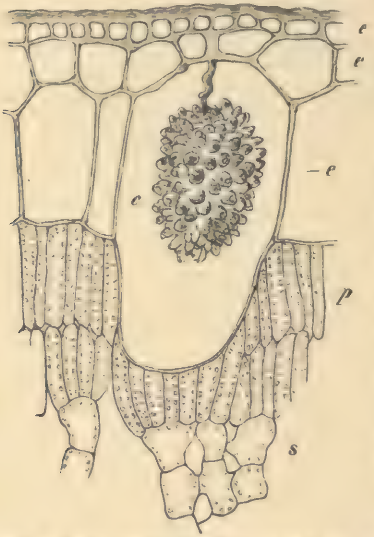


Fig. 76.—Part of transverse section of a leaf of *Ficus elastica*. *c*, Cystolith; *e*, *e*, *e*, three-layered epidermis; *p*, palisade parenchyma; *s*, spongy parenchyma. (× 240.)

The thickened bands by which such thickenings of the cell wall are effected are attached by narrowed bases to the primary membrane (49). When the membrane separates two water-conducting elements its central portion is thickened like the torus of the bordered pit. The annular and spiral types of thickening characterise the water-conducting elements of growing parts of the plant, since they allow of extension of the wall during growth. The thickening band can often be removed as a continuous spiral from the lamella to which it is attached.

COLLENCHYMATOUS cells are living cells, the walls of which are thickened principally at the corners (Fig. 74 *c*); such cells occur commonly in the more highly organised plants and form a special kind of tissue (p. 116). Cells on the surface of plants have usually only their outer walls thickened (Fig. 74 *e*).

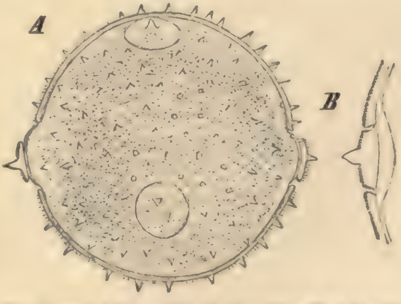


Fig. 77.—*A*, Pollen-grain of *Cucurbita Pepo* in surface view, and partly in optical section, rendered transparent by treating with oil of lemons (× 240); *B*, part of transverse section of pollen grain of *Cucurbita verrucosa* (× 540).

Unequal thickening of the cell-wall is most noticeable when it is limited to definite small areas. This is the case with those lens-shaped thickenings of the outer walls of the epidermal cells of the upper surface of foliage leaves, which are of frequent occurrence and, according to G. HABERLANDT (50), act as convex lenses to concentrate the light (Fig. 75). By the thickening of cell walls at special points, protuberances projecting into the cell cavity are formed; in this way the formations known as CYSTOLITHS arise. Certain large cells in the leaves of the India-rubber plant (*Ficus elastica*) contain peculiar clustered bodies, formed by the thickening of the cell wall at a single point (Fig. 76). In their formation a stem-like body or stalk first protrudes from the cell wall; by the addition of freshly deposited layers this becomes club-shaped, and, by continued irregular deposits, it finally attains its clustered form.

So far only centripetal wall thickenings have been described. Cells, the walls of which are centrifugally thickened, can naturally only occur where the cell walls have free surfaces. The outer walls of hairs generally show small inequalities and projections. The surface walls of spores and pollen grains (Fig. 77) show a great variety of such centrifugally developed protuberances, in the form of spines, ridges, reticulations, and bands of characteristic structure.

Cell-Wall Substance (^{51}).—The most important constituent of cell walls is CELLULOSE. It is present in the cell walls of all plants, except in those of the majority of Fungi.

Cellulose is a carbohydrate of which the chemical composition is expressed by the general formula $(C_6H_{10}O_5)n$. It is insoluble in dilute acids or alkalies. By the action of concentrated sulphuric acid it is converted into dextrose. After treatment with sulphuric or phosphoric acid, iodine will colour it blue; it shows a similar reaction when exposed to the simultaneous action of a concentrated solution of certain salts, such as zinc chloride or aluminium chloride, and of iodine. Accordingly, chlor-zinc-iodide, on account of the blue colour imparted by it, is one of the most convenient tests for cellulose. GILSON (^{52}) obtained cellulose in a crystalline condition in the form of sphærites or dendrites.

The cell walls never consist entirely of pure cellulose, but contain a considerable amount of other substances, which are not stained blue by chloroiodide of zinc. In unlignified cell walls PECTIN SUBSTANCES are particularly prominent. They are easily distinguished by the readiness with which they dissolve in alkalies, after being previously acted upon by a dilute acid.

Susceptibility to certain stains—for example, congo red—is a characteristic of cellulose; while other stains, such as safranin and methylene blue, colour pectin substances more deeply. According to MANGIN (^{53}), the partition wall formed in the higher plants during cell division consists almost wholly of pectin substances; the next developed laminae, the secondary cell-wall layer, of a mixture of cellulose and pectin substances; the last formed, or tertiary layer, chiefly of cellulose. If the secondary layer of the cell wall remain unlignified, the amount of the pectin substances contained in it increases with age and helps to strengthen the MIDDLE LAMELLA, or primary cell-wall layer.

Among the substances entering into the composition of cell walls, in addition to cellulose and the pectin substances, mention must be made of CALLOSE. It is characterised by its insolubility in cuprammonia and solubility in soda solution, and in a cold 1 per cent solution of caustic potash. It is coloured a red brown by chloroiodide of zinc, with aniline blue it takes an intense blue, and with corallin (rosolic acid) a brilliant red. Its presence in the higher plants is limited to a few special cases; it envelops the sieve-pits and is always present in calcified cell-wall layers, as, for example, in cystoliths (Fig. 76). Chitin, a proteid substance, according to GILSON (^{54}), takes the same place in the cell walls of the Fungi as cellulose in the cell walls of the higher plants.

Where cell walls become LIGNIFIED or SUBERISED, it is particularly the secondary layer that receives the wood or cork substance, while the tertiary or internal layer retains its cellulose character.

Lignification depends on the introduction into the membrane of certain substances, among which, according to CZAPEK (55), an aromatic aldehyde which he names hadromal is never wanting. According to F. C. VON FABER (56) hadromal is not present in all lignified membranes, and on the other hand occurs in many that are not lignified. Associated with hadromal, according to CZAPEK, is coniferin, which can be obtained from the youngest xylem. CZAPEK denies the existence of vanillin in lignified membranes. The proportion in which hadromal is found in wood does not exceed 1·2 per cent of its dry weight. To its presence the so-called lignin reactions are due, a violet colouration with phloroglucin and hydrochloric acid, and a yellow colouration with acid anilin sulphate. The potassium permanganate reaction (a red colouration on treatment with a 1 per cent solution of that substance followed by ammonia) is, according to F. C. FABER, a general feature of lignified membranes. With chlor-zinc-iodide lignified membranes stain yellow, not blue.

Corky cell walls contain suberin and take a yellowish-brown colour with chloroiodide of zinc ; with caustic potash, a yellow. VAN WISSELINGH (57) has disputed the presence of cellulose in suberised cell walls, and regards the cork substance or SUBERIN as a fatty body, which is composed of glycerine esters and other compound esters, as well as of one or more other substances which are infusible, insoluble in chloroform, and decomposed by a solution of caustic potash.

CUTINISATION, which is similar to but not identical with suberisation, is usually due to the subsequent deposition of cutin in cellulose cell walls.

VAN WISSELINGH has shown that phellonic acid, which is always present in suberin, is constantly absent in cutin. The behaviour of cutin, as of suberin, varies according to the source from which it is derived. Cutin withstands better the action of caustic potash. In other respects, the reactions given by cutinised cell walls with chloroiodide of zinc or solutions of caustic potash are almost identical with those of suberised cell walls.

Young cell walls are less elastic, but relatively more extensible than older ones. The power of resisting a stress is increased by lignification. The presence of cutinised and corky membranes at the surface of the plant diminishes the loss of water from it (58).

The layers of the cell walls of some cells, particularly the superficial cells of certain fruits, as of Sage, and of numerous seeds, such as Flax and Quince seeds, become mucilaginous, and swell in water to MUCILAGE, which, according to G. KLEBS (59), serves the purpose of attaching the seeds to the soil. Firm cell walls can also be transformed into GUM, as is so often apparent in Cherry and Acacia trees, portions of the wood of which often succumb to GUMMOSIS.

The several varieties of gums and mucilage react differently, according as they are derived from cellulose, callose, pectin substances, or from allied substances. According to MANGIN they may be microchemically distinguished by their reaction with ruthenium red, which stains only such as are derived from pectin substances or related substances, such as the mucilage of the seeds of the Cruciferae and Quince (*Cydonia*), that from the mucilage cells of the Malveae, the gums of the Cherry and Acacia, the gum tragacanth from *Astragalus gummifer*. The mucilage of Orchid tubers, on the other hand, is related to cellulose, and remains uncoloured with the same reagent.

The cell walls of the seeds of many Palms, as also those of *Ornithogalum* (Fig. 71), have strongly developed thickening layers, which are full of pits. These thickening layers are lustrous white, and, as in the case of the seeds of the Palm, *Phytelephas macrocarpa*, may attain such a degree of hardness as to be technically valuable as vegetable ivory. Such thickening layers may contain other carbohydrates in addition to cellulose, and by the action of ferments are dissolved during germination. They are accordingly to be considered as a reserve substance of the seeds.

Cell walls often become coloured by tannin or derivative substances; in this way, for instance, the dark colour is produced which is often seen in the coats of seeds and in old wood. The colours of the woods of economic value are due to such discoloured cell walls. Inorganic substances are often deposited in large quantities in old cell walls. Among such substances calcium oxalate is often met with, commonly in crystal form; also, although not so frequently, calcium carbonate. In the cystoliths of *Ficus elastica* (Fig. 76) so much calcium carbonate is deposited that it effervesces with hydrochloric acid. In many plants, as, for instance, most of the Characeae, the quantity of calcium carbonate in the cell walls is so great as to render them stiff and brittle. Silica is also present in the superficial cell walls of the Gramineae, Equisetaceae, and many other plants, and gives them a very considerable firmness. The lens-shaped thickenings in the outer walls of the epidermal cells of *Campanula persicifolia* are also silicified.

By withdrawing water from the cells a contraction of the protoplast and its consequent separation from the cell wall is brought about (see Plasmolysis). Such protoplasts are able under certain conditions to surround themselves with a new cell-membrane. The removal of the cuticle or of the waxy covering from the surface of certain plants (*Agave*, *Aloe*, *Ricinus*, *Sedum*) is followed by its regeneration ([60]).

Form of the Cell.—As cytoplasm is a viscous fluid, and would tend, if unimpeded, to take a spherical shape, it may be assumed that the natural and primary form for cells is spherical. Such a shape, however, could only be realised by cells which, in their living condition, were completely free and unconfined, or in such as were able to expand freely in all directions. Newly developed cells, in a continuous tissue, are, at first, nearly always polygonal. Through subsequent growth their shape may change. The cubical cells of the growing point either elongate to a prism or remain, owing to repeated division, short and tabular. If the growth is limited to certain regularly arranged points of the surface, they become stellate; if these points are less uniformly arranged their outline is correspondingly unsymmetrical. In consequence of energetic growth in length, fibre-like, pointed cells are developed. If the walls of such cells become much thickened, they are called SCLERENCHYMA fibres (Fig. 78 *A*). These show diagonal markings, due to their elongated pits, which are generally but few in number. When fully developed, the living contents of such cells are small in amount and frequently they contain only air. In the last case, they merely act as mechanical elements (stereides) and contribute to the rigidity of the plant as a whole. Cells somewhat similar, but shorter and considerably wider, not pointed at the ends, and provided with bordered pits, are called TRACHEIDES (Fig. 78 *B*). The tracheides, in their fully developed condition, never have any living contents, but serve as water-carriers for the plant. So long as they remain active, they contain only water and isolated air-bubbles; their active functions afterwards cease, and they become filled with air. Tracheides which are specially elongated, and at the same time have only a narrow lumen, and, like the sclerenchymatous fibres, serve merely mechanical purposes, are known as FIBRE TRACHEIDES. Very long tracheides with a wide lumen and thin walls, functioning, like typical tracheids, as water-carriers, are distinguished as vasiform or VASCULAR TRACHEIDES (Fig. 78 *C*). They are characterised by the annular, spiral, or reticulate markings of their thickening layers, and may also be provided with bordered pits. The walls of tracheides are always lignified, while those of the sclerenchyma fibres may or may not have undergone this change.

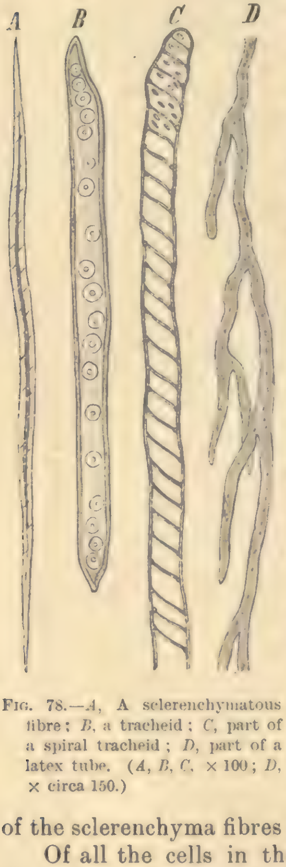


FIG. 78.—*A*, A sclerenchymatous fibre; *B*, a tracheid; *C*, part of a spiral tracheid; *D*, part of a latex tube. (*A*, *B*, *C*, × 100; *D*, × circa 150.)

Of all the cells in the more highly organised plants, the LATEX CELLS or milk cells, also spoken of as latex tubes, attain the greatest length. In the Euphorbiaceae, Moraceae, Apocynaceae, and Asclepiadaceae they arise from cells which are already differentiated in the embryo. Growing as the embryo grows, they branch with it and penetrate all its members, and may thus ultimately become many metres long. The latex cells themselves have, for the most part, unthickened, smooth, elastic walls which give a cellulose reaction. They are provided (61) with a peripheral layer of living cytoplasm and numerous nuclei. Their sap is a milky, usually white fluid, which contains gum-resins, *i.e.* mixtures of gums and resins, caoutchouc, fat and wax in emulsion. In addition, they sometimes hold in solution enzymes, leptomin, tannins, often poisonous alkaloids, and salts, especially calcium malate, also in the case of *Ficus Carica* and *Carica Papaya* peptonising ferments. Proteid granules often occur in the latex, and in the latex cells of the Euphorbiaceae there are also present peculiar dumb-bell-shaped starch grains. On exposure to the air the milky sap quickly coagulates. In the adjoining figure (Fig. 78 *D*) is shown a portion of an isolated latex cell dissected out of the stem of an Asclepiadaceous plant, *Ceropegia stapelioides*.

Special cells, which differ in form, contents, or in their peculiar wall thickenings from their neighbouring cells, are distinguished as IDIOBLASTS. If strongly thickened and lignified, they are called sclerotic cells (stone cells) or sclereides. They often contain ferments; in the Cruciferae and some other orders myrosin is thus present, while *Prunus laurocerasus* contains emulsin. For the most part they contain excreted substances such as tannins and calcium oxalate. In Fig. 85 an idioblast, containing a bundle of raphides, is represented. Idioblasts, resembling tracheides and functioning as water reservoirs, are found between the chlorophyll-containing cells in the leaves of some of the Orchidaceae and Cactaceae.

Size of Cells.—The corresponding cells of equivalent members of the same plant are usually of nearly the same size, even when the members show a variation in size.

Differentiation of the Protoplasts.—In organisms composed of one or of few cells the separate parts of the same protoplasts may under some circumstances exhibit marked differences. On the other hand, in multicellular organisms whole protoplasts are specialised for functions with the performance of which their definite structure is connected.

Inclusions of the Protoplasm—STARCH.—The chloroplasts in plants exposed to the light almost always contain starch grains. These grains of starch found in the chloroplasts are the first visible products of the assimilation of inorganic matter. They are formed in large numbers, but as they are continually dissolving, always remain small. Large starch grains are found only in the reservoirs of reserve material, where starch is formed from the deposited products of previous assimilation. Such starch is termed RESERVE STARCH, in contrast to the ASSIMILATION STARCH formed in the chloroplasts. All starch used for economic purposes is reserve starch. The starch grains stored as reserve material in potatoes are comparatively large, attaining an average size of 0·09 mm. As shown in the following figure (Fig. 79), they are plainly stratified. The stratification is due to the varying densities of the successive layers; thicker denser layers which appear clear by transmitted light alternate with thinner less dense layers which appear dark. They are excentric in structure, since the organic centre, about which the different layers are laid down, does not correspond with the centre of the grain. The starch grains of the leguminous plants and cereals, on the other hand, are concentric, and the nucleus of their formation is in the centre of the grain. The starch grains of the Kidney Bean, *Phaseolus vulgaris* (Fig. 80), have the shape of a flattened sphere or ellipsoid; they show a distinct stratification, and are crossed by fissures radiating from the centre. The disc-shaped starch grains of wheat are of unequal size, and only indistinctly stratified. A comparison of the accompanying figures (Figs. 79-81), all equally magnified, will give an idea of the varying size of the starch grains of different plants. The size of starch grains varies, in fact, from 0·002 mm. to 0·170 mm. Starch grains 0·170 mm. large, such as those from the rhizome of *Canna*, may be seen even with the naked eye, as minute bright bodies. In addition to the simple starch grains so far described, half-compound and compound starch grains are often found. Grains of the former kind are made up of two or more individual grains, surrounded by a zone of peripheral layers enveloping them in common. The compound grains consist merely of an aggregate of individual grains unprovided with any common enveloping layers. Both half-compound (Fig. 79 *B*) and compound

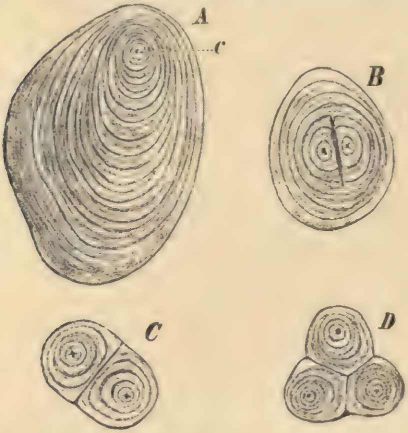


FIG. 79.—Starch grains from a potato. *A*, simple; *B*, half-compound; *C* and *D*, compound starch grains; *c*, organic centre of the starch grains, or nucleus of their formation. (× 540.)

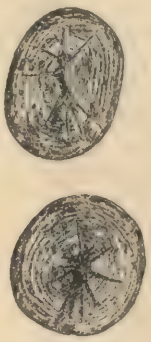


FIG. 80.—Starch grains from the cotyledons of *Phaseolus vulgaris*. (× 540.)

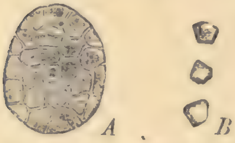


FIG. 81.—Starch grains of the oat, *Avena sativa*. *A*, Compound grain; *B*, isolated component grains of a compound grain. (× 540.)

starch grains (Fig. 79 *C*, *D*) occur in potatoes, together with simple grains. In oats (Fig. 81) and rice all the starch grains are compound. According to Nägeli (62), the compound starch grains of rice consist of from 4 to 100 single grains; those of the oat of about 300, and those of *Spinacia glabra* sometimes of over 30,000. Starch thus formed from previously assimilated organic substances also requires chromatophores for its production. The grains are formed by means of leucoplasts, which are, in consequence, often termed STARCH-BUILDERS. If the starch grain is uniformly surrounded by the leucoplast during its formation it grows uniformly on all sides and is symmetrical about its centre. If the formation of a starch grain should begin near the periphery of a leucoplast, the grain would grow more rapidly on the side on which the main mass of the leucoplast is present and the starch grain thus becomes excentric (Fig. 82). Should, however, several starch grains commence to form at the same time in one leucoplast, they would become crowded together and form a compound starch grain, which, if additional starchy layers are laid down, gives rise to a half-compound grain.

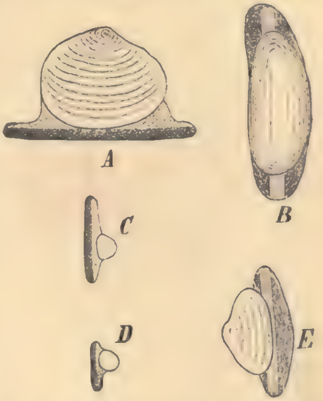


Fig. 82.—Leucoplasts from an aerial tuber of *Phajus grandifolius*. *A*, *C*, *D*, *E*, viewed from the side; *B*, viewed from above; *E*, leucoplast becoming green and changing to a chloroplast. (× 540.)

It has been asserted that starch grains are crystalline bodies, so-called sphærites (63), and are composed of fine, radially arranged, needle-shaped crystals, which A. Meyer terms trichites. Their stratification, according to this view, is due to variations in the form and number of the crystal needles in the successive layers. On the other hand, H. Fischer (64) has explained the stratification as due to zonal splits rich in water, which originate by contraction taking place in the substance of the grain at some distance from its growing surface. Henry Kraemer (65) holds that a crystalloid and a colloid substance are present, but are united in different proportions in the successive lamellæ of the starch grain. In a few individual cases, Arthur Meyer has succeeded in showing that the stratification of the starch grains corresponds to the alternation of the periods of day and night, *i.e.* to the interference which is thus caused in the nutritive processes. The growth of starch grains is also, according to him, affected by the solvent action of surrounding substances, whereby the peripheral layers may be partially removed, and then no longer completely envelop the entire grain. Starch grains are composed of a carbohydrate, the formula of which is $(C_6H_{10}O_5)n$. Most starch-grains consist of amylose and are coloured blue with iodine; in addition to this they contain, according to L. Maquenne and Eug. Roux (66), a mucilaginous substance which they term amylo-pectin. The presence of this substance causes the pasty union of the starch-grains when treated with boiling water or alkalies. The grains swell in water of 60°-70° C., are but little soluble in water at 100° C., but are rapidly dissolved by super-heated water at 140°-150° C. Starch swells very readily at ordinary temperatures in solutions of potassium, or sodium hydrate. Heated without addition of water, *i.e.* roasted, starch becomes transformed into dextrin, and is then soluble in water and correspondingly more digestible. The glutinous starch of varieties of Rice and Millet (*Oryza sativa*, var. *glutinosa*, *Sorghum vulgare*, *glutinosum*) is in the completely unswollen condition coloured brown with iodine; when swollen by a dilute solution of iodine, it takes a red, wine-red, or purple colour. According to O. BÜTSCHLI (67) it consists of amyloerythrin, a carbohydrate resembling starch. In polarised light, starch grains, like inorganic sphærites, show a dark cross. This appearance is usually referred to the doubly refractive nature of the elements of which the starch grain is constructed.

The amount of starch contained in reservoirs of reserve material is often considerable; in the case of potatoes 25 per cent of their whole weight is reserve starch, and in wheat the proportion of starch is as high as 70 per cent. The starch flour of economic use is derived by washing out the starch from such reservoirs of reserve starch. In the preparation of ordinary flour, on the contrary, the tissues containing the starch are retained in the process of milling.

Aleurone.—Aleurone or proteid grains are produced in the seeds of numerous plants, especially in those containing oil. They are formed from vacuoles, the contents of which are rich in albumen, and harden into round grains or, sometimes, into irregularly shaped bodies. The albuminous substances of which they consist are, according to A. TSCHIRCH and H. KRITZLER (68), mainly globulins. A portion of the albumen often crystallises, so that frequently one and occasionally several crystals are formed within the aleurone grain. In aleurone grains containing albumen crystals there may often be found globular bodies, termed GLOBOIDS, which, according to PFEFFER (69), consist of a double phosphate of magnesium and calcium in combination with some organic substances. Crystals of calcium oxalate are also found enclosed in aleurone grains.

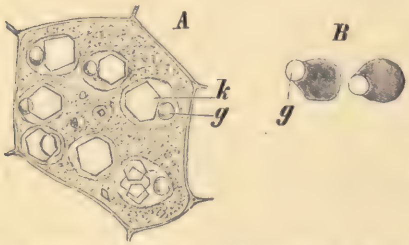


FIG. 83.—*A*, Cell from the endosperm of *Ricinus communis*, in water; *B*, isolated aleurone grains in olive oil; *k*, albumen crystals; *g*, globoid. (× 540.)

The seeds of *Ricinus* (Fig. 83) furnish good examples of aleurone grains with enclosed albumen crystals and globoids. The aleurone grains themselves lie embedded in a cytoplasm that is rich in oil. In the cereals the aleurone grains which lie only in the outer cell layer of the seeds (Fig. 84 *al*) are small, and free from all inclusions; they contain neither crystals nor globoids. As the outer cells of wheat grains contain only aleurone, and the inner almost exclusively starch, it follows that flour is the richer or poorer in albumen, the more or less completely this outer layer has been removed before the wheat is ground. From the inner layers finer and whiter flour can be made: while more nourishing flour is obtained from the outer layers. Reactions for aleurone are the same as those already mentioned for the albuminous substance of protoplasm. Treatment of a cross-section of a grain of wheat (Fig. 84) with a solution of iodine would give the aleurone layer a yellow-brown colour, while the starch layers would be coloured blue.

ALBUMEN CRYSTALS.—Crystals of albumen are of relatively frequent occurrence in vegetable tissues and are often found in aleurone grains (Fig. 83). Their appearance in the seed of *Ricinus* has been described above, and especially large crystals are found in the endosperm of the Brazil nut (*Bertholletia excelsa*) belonging to the Lecythidaceae. They have previously been mentioned as occurring in the chromatophores. In the illustration of the leucoplasts of *Phajus grandifolius* (Fig. 82), the rod-shaped crystals are represented as light stripes (in *B* and *E*). Albumen crystals may also occur directly in the cytoplasm; as, for instance, in the cells poor in starch, in the peripheral layers of potatoes. Albumen crystals are sometimes found even in the cell nucleus. This is particularly the case in the Toothwort (*Lathraea squamaria*), and in many Scrophulariaceae and Oleaceae (70). Albumen crystals usually belong either to the regular or to the hexagonal crystal system. They differ from other crystals in that, like dead albuminous substances, they may be stained, and also in that they are capable of swelling by imbibition. Subjected to the action of water or a dilute solution of caustic potash, they at first increase in size without losing their crystalline outline.

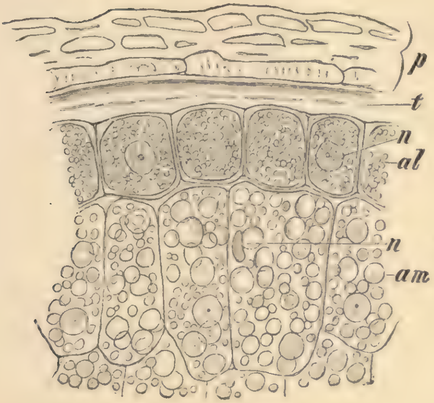


FIG. 84.—Part of a section of a grain of wheat, *Triticum vulgare*. *p*, Pericarp; *t*, seed coat, internal to which is the endosperm; *al*, aleurone grains; *am*, starch grains; *n*, cell nucleus. (× 240.)

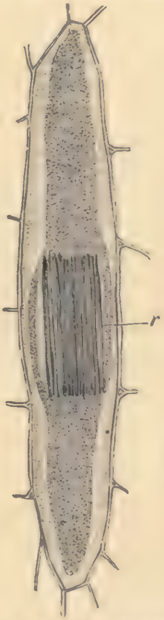


FIG. 85.—Cell from the cortex of *Dracaena rubra*, filled with mucilaginous matter and containing a bundle of raphides, *r*. (× 160.)

Crystals of Calcium Oxalate.—Few plants are devoid of such crystals. They are formed in the cytoplasm, within vacuoles which afterwards enlarge and sometimes almost fill the whole cell. In such cases the other components of the cell become greatly reduced; the cell walls at the same time are often converted into cork, and the whole cell becomes merely a repository for the crystal. The crystals may be developed singly in a cell, in which case they are of considerable size and can be seen to belong either to the tetragonal or monosymmetrical crystal system; or the crystals are so small and numerous that their form cannot be clearly made out and they appear as a crystalline sand filling the cell. Frequently they form CRYSTAL AGGREGATES, clusters of crystals radiating in all directions from a common centre. In the Liliaceae, Orchidaceae, and other Monocotyledons, compact bundles of needle-shaped crystals of calcium oxalate, the so-called RAPHIDES, are especially frequent (Fig. 85). Such crystal bundles are always enclosed in a large vacuole filled with a mucilaginous substance. The degree of concentration of the mother liquor from which the crystals have separated, determines, according to KNY (71), their form, whether tetragonal or monoclinic.

SILICEOUS BODIES, which are only soluble in hydrofluoric acid, are found in the cytoplasm of many cells, especially of Palms and Orchids, and often completely fill the whole cell.

TANNIN.—Highly refractive vacuoles filled with a concentrated solution of tannin are of frequent occurrence in the cytoplasm of cortical cells, and may often grow to a considerable size. The dark-blue or green colour reaction obtained on treatment with a solution of ferric chloride or ferric sulphate, and the reddish-brown precipitate formed with an aqueous solution of potassium bichromate, are usually accepted as tests for the recognition of tannin, although equally applicable for a whole group of similar substances.

FATS and OILS in plants are mixtures of fatty-acid esters. Frequently, as in most Monocotyledons, a fatty oil appears in the old chlorophyll grains. The occurrence of castor oil in the form of highly refractive drops in the cytoplasm of the aleurone-containing cells in the endosperm of the castor-oil seeds, has already been referred to. Oil usually occurs in this form. But fatty substances may also appear in the cytoplasm as irregularly shaped, more or less soft grains, as for example in the vegetable butters and in the wax of various seeds; they may even be crystalline, as in the needle-like crystals of Para-nuts (*Bertholletia excelsa*) and of Nutmeg (*Myristica fragrans*). Special cytoplasmic structures in which the drops of oil are embedded, are of frequent occurrence in the epidermal cells of Orchidaceae and Liliaceae and go by the name of elaioplasts (72).

CHOLESTERIN.—Since this substance is a regular constituent especially of green cells, it probably plays an important part in metabolism (73).

GLYCOGEN.—This substance (74), related to starch, and of frequent occurrence in animal tissues, fulfils, according to ERRERA (75), the same functions in the Fungi as sugar and starch in the higher plants. Cytoplasm containing glycogen is coloured a reddish brown with a solution of iodine. This colour almost wholly disappears if the preparation be warmed, but reappears on cooling.

ETHEREAL OILS AND RESINS.—In many cases the strongly refractive drops found dispersed throughout the cytoplasm are globules of some ethereal oil. It is the presence of such oils in the petals of many flowers that gives to them their agreeable perfume. Under certain conditions the oil globules may become crystallised. This occurs, for example, in Rose petals. In most cases ethereal oils or resins are formed in special protuberances (76) or strata (77) of the cell wall and only later are stored in the interior of the cell or in special intercellular spaces formed by separation or destruction of cells. Special cells of this kind, often with corky walls and filled with resin or ethereal oils, are found in the rhizomes of certain plants, as for instance in those of *Acorus Calamus* and of Ginger (*Zingiber officinale*): also in the bark, as, for example, of Cinnamon trees (*Cinnamomum*); in the leaves, as in the Sweet Bay (*Laurus nobilis*); in the pericarp and seed of the Pepper (*Piper nigrum*); in the pericarp of Anise (*Illicium anisatum*).

MUCILAGE is often found in the cells of bulbs, as in *Allium Cepa* and *Urginea Scilla*, in the tubers of Orchids, also in aerial organs, especially in the leaves of succulents, which, living in dry places, are thus enabled to maintain their water supply by means of their mucilaginous cells.

CAOUTCHOUC AND GUTTA-PERCHA.—These substances are found in a number of plants belonging to different groups, in particular in the Moraceae, Euphorbiaceae, and Sapotaceae. They occur in the latex of special cells in the form of small globules, which, suspended in the watery sap, give it its milky appearance.

FERMENTS.—Bodies of this nature are widely spread in vegetable cells. Their significance in the oxidation processes taking place in the organism has been dealt with by R. CHODAT, A. BACH (78), and others. The name leptomin was given by RACIBORSKI (79) to a catalytic enzyme, which he found in the sieve-tubes and laticiferous elements of the higher plants, in the milk of the coco-nut, and in the tissues of the potato tuber.

SULPHUR.—The presence of sulphur in the form of small refractive grains in the protoplasm of certain Bacteria, the Beggiatoae, is noteworthy. These Bacteria live in water containing much organic matter, and, according to WINOGRADSKY (80), obtain their sulphur from sulphuretted hydrogen. In fulfilling its function in the Bacteria the sulphur becomes oxidised into sulphuric acid.

The Cell Sap.—Under this term is included especially the fluid which in old cells fills the inner sap cavity. It is generally more watery and clearer than the fluid contained in the smaller vacuoles of the cytoplasm. No sharp distinction can, however, be drawn between the sap cavity and vacuoles, and, moreover, a number of such vacuoles may take the place of the sap cavity itself. The cell sap usually gives an acid reaction, owing to the presence in it of organic acids or their salts. The substances held in solution by the cell sap are very various. The soluble carbohydrates, in particular the sugars (cane sugar, the glucoses, and especially grape sugar), frequently occur in the cell sap. The glucoses may be recognised by their reducing properties.

If preparations containing glucose be placed in a solution of copper sulphate, and, after being washed out, are transferred to a solution of caustic potash and heated to boiling, they will give a brick-red precipitate of cuprous oxide. If cane sugar or saccharose be present, this same treatment gives only a blue colour to the cell sap.

Carbohydrates are transported in a plant principally in the form of glucose; cane sugar, on the contrary, is stored up as a reserve material, as for example, in the sugar-beet, in the stems of sugar-cane, and in other plants from which the sugar of economic use is derived.

INULIN, a carbohydrate in solution in cell sap, behaves in the same way in the Compositae. Treated with alcohol, inulin is precipitated in the form of small granules, which may be redissolved in hot water. When portions of plants containing much inulin, such as the root tubers of *Dahlia variabilis*, are placed in alcohol or dilute glycerine, the inulin crystallises out and forms sphærites, spheroidal bodies composed of radiating crystal needles arranged in concentric layers. Amides such as GLUTAMIN and ASPARAGIN are also generally present in the cell sap. There are frequently found dissolved in the cell sap TANNINS, ALKALOIDS, and GLUCOSIDES, such as coniferin, hesperidin, amygdalin, solanin, æsculin, saponin, and also bitter principles related to the glucosides. Organic acids (malic, formic, acetic, and oxalic acids) are also of frequent occurrence in the cell sap; thus, malic acid is usually present in the leaves of the succulents. For the most part, these organic acids unite with bases, and the salts which are formed often crystallise. Of acid salts, which are less frequent than free acids, the binoxalate of potassium found in Field Sorrel (*Rumex*) and Wood Sorrel (*Oxalis*) deserves special mention. Species of *Salicornia* and *Salsola* contain sodium oxalate. The cell sap always contains dissolved inorganic salts, especially nitrates, sulphates, and phosphates. The different vacuoles of the same protoplast may have distinct contents; thus one may contain tannin and another be free from it, or one may have coloured and another colourless sap.

The cell sap is often coloured, principally by the so-called ANTHOCYANIN, which Hans Molisch, at least in some cases, regards as being a non-nitrogenous glucoside (81). This is blue in an alkaline, and red in an acid reacting cell sap, and, under certain conditions, also dark red, violet, dark blue, and even blackish-blue. Anthocyanin can be obtained from the super-saturated cell sap of a number of deeply coloured parts of plants in a crystalline or amorphous form. Blood-coloured leaves, such as those of the Copper Beech, owe their characteristic appearance to the united presence of green chlorophyll and anthocyanin. The different colours of flowers are due to the varying colour of the cell sap, to the different distribution of the cells containing the coloured cell sap, and also to the different combinations of dissolved colouring matter with the yellow, orange, or red chromoplasts and the green chloroplasts. There is occasionally found in the cell sap a yellow colouring mattter known as xanthëin; it is nearly related to xanthophyll, but soluble in water.

2. ONTOGENY OF THE CELL

The Origin of the Living Elements of Protoplasm.—All the nuclei in an organism owe their origin to the nuclei of previous generations. The spontaneous formation of a nucleus never takes place. In the same manner, the cytoplasm of every organism is derived from the cytoplasm of the germ cell, and, so far as is yet known, the chromatophores take their origin only from their own kind.

Nuclear Division.—Except in a few limited cases, nuclei reproduce themselves by MITOTIC or INDIRECT DIVISION. This process, often referred to as KARYOKINESIS, is somewhat complicated, but seems necessary in order to effect an equal division of the substance of the mother nucleus between the two new daughter nuclei.

Indirect Nuclear Division ([82]).—In its principal features the process is similar in the more highly organised plants and in animals. Its stages are represented in a somewhat diagrammatic manner in the following figure (Fig. 86), as they occur in a vegetative cell such as those which compose the growing point.

The fine network of the resting nucleus (Fig. 86, 1 *n*) becomes drawn together at definite points and separated into a number of bodies (Fig. 86, 2 *ch*), the outline of which is at first irregular. Their form soon becomes filamentous, and the filaments become denser and at the same time shorter and thicker (3), and stain more deeply. The stainable substance of the filament, which is called chromatin, becomes arranged in more or less regular transverse discs united by linin (3). The filaments themselves are called CHROMOSOMES (Fig. 86, 3, 4). The chromosomes are moved into the plane of division where they constitute the nuclear or equatorial plate (5 *kp*, 6, 7). Each chromosome has meanwhile undergone a longitudinal split which continues to become more marked (5, 6, 7). The two halves of each chromosome thus separated move away from one another in opposite directions, and take part in the formation of the daughter nuclei (9 *t*).

Other changes serve to direct the process thus briefly described. While the nuclear network is separating into the individual chromosomes, cytoplasmic filaments become applied to the nuclear membrane, surrounding it with a fibrous layer. This layer becomes raised up from the nuclear membrane at two opposite points (3 *k*) and forms the polar caps. These are filled with a homogeneous substance in which fine filaments appear later. The latter converge at the poles, without, however, coming into contact; they constitute two pointed bundles, since they diverge from one another as they pass from the polar regions (4 *k*). At this stage the nucleoli (*nl*) are dissolved and the nuclear membrane disappears. The fibres proceeding from the polar caps can thus become prolonged into the nuclear cavity (4, 5). Here they either become attached to the chromosomes, or filaments from the two poles may come into contact and extend continuously from the one pole to the other. In this way the nuclear spindle is formed (5, 6, 7). The fibres of the spindle attached to the chromosomes may be termed traction-fibres, those which run from pole to pole supporting-fibres. The nucleoli appear to form a reserve substance which serves to nourish the chromosomes and, later, has the special duty of providing material for the formation of the spindle. Any excess of nucleolar substance passes into the surrounding cytoplasm, where it forms the

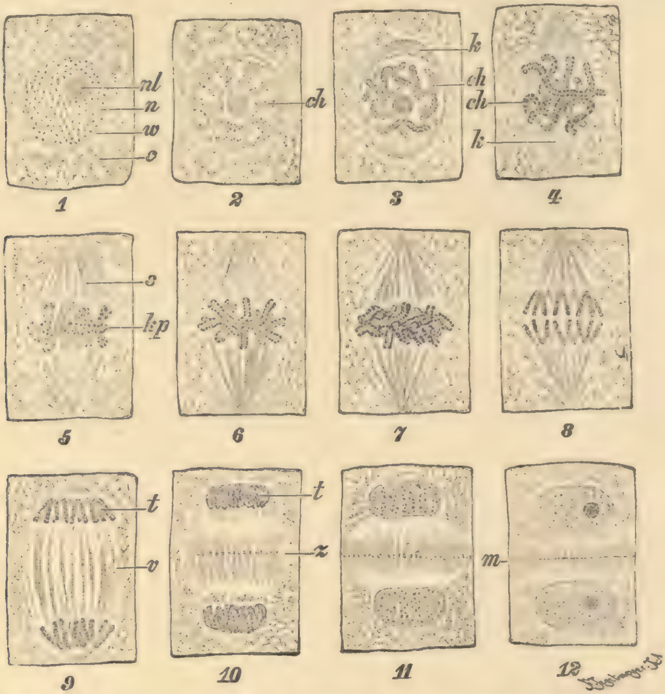


FIG. 86.—Successive stages of nuclear- and cell-division in a meristematic cell. *n*, Nucleus; *nl*, nucleolus; *w*, nuclear membrane; *c*, cytoplasm; *ch*, chromosomes; *k*, polar caps; *s*, spindle; *kp*, nuclear plate; *t*, young daughter nuclei; *v*, connecting fibres: *z*, cell-plate; *m*, new cell wall. In 1, the resting nucleus; 2 and 3, separation of the chromosomes; 4, chromosomes with transverse discs; 5, the arrangement of the chromosomes to form the cell plate and their longitudinal fission; 3-5 show the formation of the spindle from the polar caps; 6, the longitudinal fission of the chromosomes; 7, the beginning of their separation to either pole; 8, the complete separation of the daughter chromosomes; 9, passage of the daughter chromosomes to either pole; 10-12, formation of the daughter nuclei; in 9-11 the origin of the connecting fibres and of the cell plate is seen, while in 12 the new cell-wall is formed. (× about 600.)

so-called extranuclear nucleoli. The traction-fibres promote the arrangement of the chromosomes in the equatorial plane (5). After the chromosomes have split longitudinally into the daughter chromosomes, the latter are separated and drawn towards the two poles by the contraction of the traction-fibres (8, 9). The supporting-fibres afford the necessary resistance in the process. The spindle fibres can often be traced to the limiting layer of the cytoplasm, and their attachment to this determined. In forming the daughter nuclei, the free ends of the chromosomes first become drawn in (10), and the surrounding cytoplasm separates itself by means of a protoplasmic membrane, the nuclear membrane (11), from the developing nuclei. Within the nuclear cavities which are thus produced the chromosomes again assume a reticulate structure and unite with one another to form a network within which their individual limits are not distinguishable. We are compelled, however, to assume that the individuality of the chromosomes is not lost (83). The young nuclei enlarge, the extranuclear nucleoli disappear in the surrounding cytoplasm, and one or more nucleoli at length appear in the nuclei; finally the resting condition is again attained.

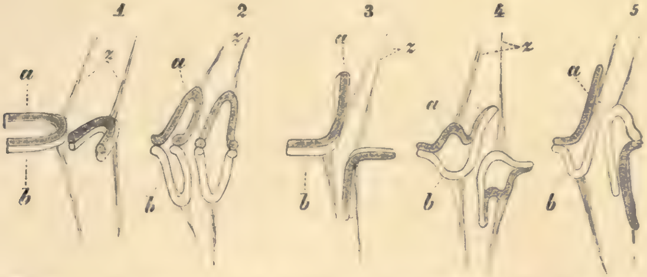


FIG. 87.—Diagrammatic representation of the different positions occupied by the chromosomes in the spindle and during their separation. *a* and *b*, daughter chromosomes of one mother chromosome ; *z*, traction-fibres of the spindle.

The process of nuclear division is described above as it usually takes place in the young tissues of more highly organised plants. The chromosomes are usually loop-shaped, and the traction-fibres become attached to the middle point of the loop, less commonly toward an end. The traction-fibres from the two poles attach themselves respectively to the two daughter chromosomes of each pair. The orientation of the pairs of daughter chromosomes in the nuclear spindle, and the way in which they separate from one another, are represented in the accompanying diagram (Fig. 87). In (1) the two shanks of each pair of chromosomes lie nearly in the equatorial plane, and each of the daughter chromosomes on their separation (2) assumes the form of the letter U, remaining attached by the shanks. More commonly, while one of the shanks of the paired chromosome lies in the equatorial plane, the other is directed towards one of the two poles (3). In this case a condition of things results, when the daughter chromosomes separate, which is represented in 4 or 5. The former shows the resulting appearance when the daughter chromosomes remain for a time attached to one another at both ends; the latter when separation soon follows at the end directed towards the nuclear pole. In all cases the separation proceeds from the point of attachment of the traction-fibres. When a paired chromosome is attached to the spindle near one of its ends, the separation of the daughter chromosomes naturally commences near this end; when the attachment is by the middle of the chromosome the daughter chromosomes remain longer attached by their ends. In Fig. 86 the behaviour of the chromosomes is represented as in the diagrams 3 and 4 (Fig. 87). As a rule it does not appear so clearly, but more or less combined with the other type.

The changes occurring in a mother nucleus preparatory to division are termed the PROPHASES of the karyokinesis. These changes extend to the formation of the nuclear plate, and include also the process of the longitudinal division of the chromosomes. The stage of the nuclear plate is the METAPHASE. The separation of the daughter chromosomes is accomplished in the ANAPHASE, and the formation of the daughter nuclei in the TELOPHASE of the division. The real purpose of the whole process is attained in the quantitative and qualitative division of the chromosomes, resulting from their longitudinal splitting (Fig. 86, 5, 6, 7; Fig. 87). The anaphases and telophases of the karyokinesis are but a reverse repetition of the prophases.

The number of chromosomes occurring in any nucleus is a definite one, and when a deviation from the usual number is met with, it is due to some of the chromosomes having remained united end to end. The smallest number of chromosomes which has yet been found in the nuclei of vegetative cells of the more highly organised plants has been eight; as a rule the number is larger, amounting often to several times this number.

A special type of nuclear division, to which the name of REDUCTION DIVISION is given, is met with in those reproductive cells which start a new generation, such as the spore-mother-cells of the higher Cryptogams and Phanerogams. In the prophase of this division the chromosomes become united in pairs (Fig. 88, 1, 2), and there then occurs a marked contraction of the nuclear contents, which is characteristic of this process of division and is called SYNAPSIS (3). After this the double chromosomes become again loosened out as a delicate double thread (4), which soon unites to a correspondingly stout thread, forming a loose skein (5). The doubled nature of this thread soon becomes recognisable again (6). The skein consisting of the as yet unbroken double thread now falls into segments (7), each of which corresponds to one paired chromosome. The number of these segments is half as great as the number of chromosomes in the tissue cells of the same plant, since two chromosomes are represented by each segment. The paired chromosomes become shorter and thicker and are distributed around the periphery of the nucleus; this is the condition that has been termed diakinesis (8). At this stage kinoplasmic filaments are becoming applied to the nuclear membrane (8); the latter disappears and the nuclear spindle, which is at first multipolar (9), but ultimately becomes bipolar (10), originates from the kinoplasmic fibres. The paired chromosomes become attached to the fibres of the spindle and arranged in an equatorial nuclear plate (10). Shortly afterwards the separation of the chromosomes, until now united in pairs, takes place (11). In this process, in which the essential of the reduction division is effected, it is not longitudinal halves of chromosomes but entire chromosomes which separate from one another. The result of this is that each daughter nucleus receives only half as many chromosomes as were found in the tissue cells of the

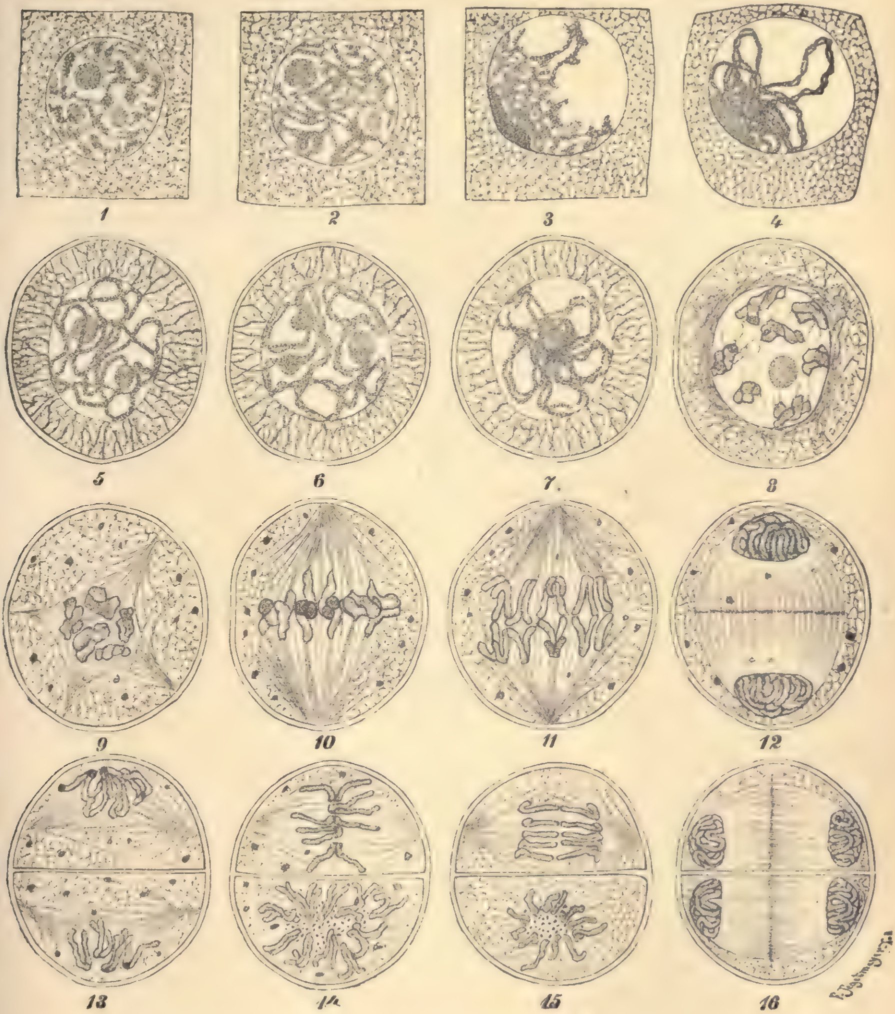


FIG. 88.—Dividing pollen-mother-cells of a Lily, somewhat diagrammatic. 1, Mother-cell with resting nucleus; 2, the separation of the chromosomes; 3, synapsis; 4, double filament in process of fusion; 5, spirem consisting of an apparently single filament derived from the fused double filament; 6, reappearance of the longitudinal split, the spirem still unsegmented; 7, spirem transversely segmented, into paired chromosomes; 8, diakinesis; 9, multipolar spindle; 10, spindle of the mother-nucleus, the nuclear plate composed of paired chromosomes; 11, reduction division, the separating chromosomes showing partial separation of their longitudinal halves; 12, young daughter nuclei; 13, the longitudinal halves of the chromosomes (daughter chromosomes) are arranged in pairs on the nuclear spindles; 14, the spindles of the daughter nuclei; 15, separation of the daughter chromosomes; 16, young stage of the grand-daughter nuclei. (× about 800.)

same plant. During their passage towards the poles of the spindle a longitudinal split can be detected in each chromosome. This split was indeed already complete in the prophase before the nuclear plate was formed, but was not followed as in an ordinary division by a separation of the halves. The two halves of each chromosome remain on the other hand in relation to one another and pass to the ? same daughter nucleus. The formation of the daughter nuclei is completed (12) as in an ordinary division, but following promptly on the first reduction division, which is also known as the HETEROTYPE division, comes a second or HOMOTYPE division (84). In this no new longitudinal splitting of the chromosomes takes place, but the two halves of each chromosome, which existed in the daughter nuclei, become separated from one another, and become the chromosomes of the grand-daughter nuclei.

The steps of this homotype division agree in other respects with those of an ordinary nuclear division, and will be clear from Fig. 88, 13-16. In 13 an early stage and in 14 the completed condition of the spindles of the dividing daughter nuclei are seen; 15 shows the division of the nuclear plate, and in 16 the young grand-daughter nuclei are completed. One of the characteristic features of the whole process is that the two divisions succeed one another immediately or very quickly. The heterotype and homotype nuclear divisions, which may together be termed the ALLOTYPIC division, may be contrasted with the ordinary or typical nuclear division. At a particular stage of development corresponding phenomena to those of the allotypic division are met with in animals as well as plants.

The smallest reduced number of chromosomes known for the nuclei of the more highly organised plants is four, *i.e.* the half of the smallest number met with in the tissue cells.

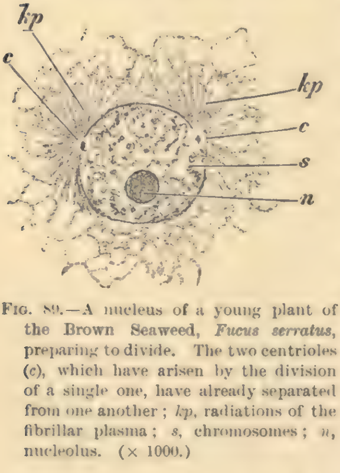


FIG. 89.—A nucleus of a young plant of the Brown Seaweed, *Fucus serratus*, preparing to divide. The two centrioles (*c*), which have arisen by the division of a single one, have already separated from one another; *kp*, radiations of the fibrillar plasma; *s*, chromosomes; *n*, nucleolus. (× 1000.)

In those lower Cryptogams, the nuclei of which possess an individualised centriole, the latter undergoes division into two at the beginning of karyokinesis. The two halves separate from one another (Fig. 89 *c*) and ultimately reach the points which will become the poles of the spindle. Round such centrioles a definite portion of protoplasm forming the centrosome is usually marked off, and around this kinoplasmic radiations (*kp*) form an astrosphere. When the centrioles have reached the poles the nuclear membrane disappears, and spindle fibres appear in the nuclear cavity itself. These clearly proceed from the centrosomes and become attached to the chromosomes. The complete nuclear spindle (Fig. 90) has a centrosome with kinoplasmatic radiations (*kp*) at each pole, but in other respects agrees with the spindles of the higher plants, from which centrioles are absent. The main features of the division and the formation of the daughter nuclei are also similar in the two cases. The centrioles persist in the daughter nuclei and divide into two on each subsequent nuclear division; the kinoplasmatic radiation around the centrosome is, however, only present during the karyokinetic process (85).

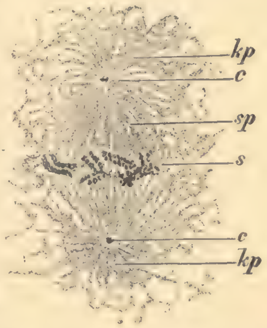


FIG. 90.—A nuclear spindle of a cell of a young plant of the Brown Seaweed *Fucus serratus* with split chromosomes in the nuclear plate. *c*, Centrioles *kp*, radiations of fibrillar plasma astrospheres; *sp*, spindle fibres; *s*, longitudinally divided chromosomes forming the nuclear plate. (× 1000.)

Direct Nuclear Division.—In addition to the mitotic or indirect nuclear division there is also a DIRECT or AMITOTIC division, sometimes called FRAGMENTATION (Fig. 91). This may have been the original mode of nuclear division, and among the lowest organisms transitions between it and indirect division are found. In the higher plants direct division of the nucleus is a reduced, or indeed a senile process which usually occurs in old cells, or in cells in which the cell contents become disorganised shortly after the nuclear division.

Instructive examples of direct nuclear division are afforded by the long internodal cells of the Stoneworts (Characeae), and also by the old internodal cells of *Tradescantia* (Fig. 91). The direct nuclear division is chiefly a process of constriction which, however, need not result in new nuclei of equal size. In the case of the Stoneworts, after a remarkable increase in the size of the nucleus, several successive rapid divisions take place, so that a continuous row of bead-like nuclei results. The old internodal cells of *Tradescantia* (Fig. 91) very frequently show half-constricted nuclei of irregular shape. While in uninuclear cells indirect nuclear division is, as a rule, followed by cell division, this is not the case after direct nuclear division.

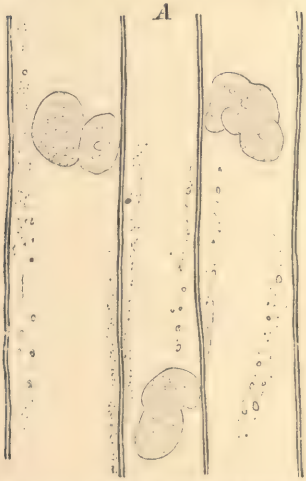


FIG. 91.—Old cells from the stem of *Tradescantia virginica*, showing nuclei in process of direct division. (× 540.)

Cell Division.—In the uninuclear cells of the higher plants cell division and nuclear division are, generally, closely associated. The supporting fibres of the spindle extending from pole to pole persist as CONNECTING FIBRES between the developing daughter nuclei (Fig. 86, 9 *v*; Fig. 88, 12, 16), and their number is increased by the interposition of others (Fig. 86, 10). In consequence of this a barrel-shaped figure is formed, which either separates entirely from the developing daughter nuclei, or remains in connection with them by means of a peripheral sheath, the CONNECTING UTRICLE. The first is the case in cells rich in cytoplasm, the latter when the cells are more abundantly supplied with cell sap. At the same time the connecting fibres become thickened (Fig. 86, 10) at the equatorial plane, and the short rod-shaped thickenings form what is known as the CELL PLATE. In the case of cells rich in protoplasm or small in diameter, the connecting fibres become more and more extended, and touch the cell wall at all points of the equatorial plane (Fig. 86, 11). The elements of the cell plate unite and form a cytoplasmic limiting layer, which then splits into two. In the plane of separation the new partition wall is formed of cell-wall substance, and thus SIMULTANEOUSLY divides the mother cell into two daughter cells (Fig. 86, 12). If, however, the mother cell has a large sap cavity, the connecting utricle cannot at once become so extended, and the partition wall is then formed SUCCESSIVELY (Fig. 92). In that case, the partition wall first commences to form at the point where the utricle is in contact with the side walls of the mother cell (Fig. 92 *A*). The protoplasm then detaches itself from the part of the new wall in contact with the wall of the mother cell, and moves gradually across until the septum is completed (Fig. 92 *B* and *C*); the new wall is thus built up by successive additions from the protoplasm.

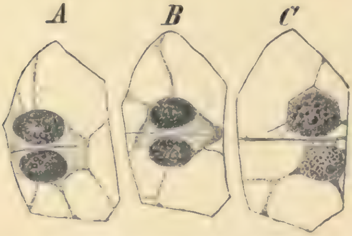


FIG. 92.—Three stages in the division of a living cell of *Epipactis palustris*. (After TREUB, × 365.)

The connecting fibres of the spindle consist of kinoplasm. The origin of the cell plate from swellings of these fibres indicates its kinoplasmatic nature also. By the splitting of the cell plate the limiting layers of the two sister cells are completed across the place of separation. The separation of the complex of connecting fibres into two halves effects an equal division of the kinoplasm between the two new cells.

In the Thallophytes, even in the case of uninuclear cells, the partition wall is not formed within connecting fibres, but arises either simultaneously from a previously formed cytoplasmic plate, or successively, by gradual projection inwards from the wall of the mother cell. It was a division process of this kind (Figs. 93, 94), first investigated in fresh-water Algae, that gave rise to the conception of cell division, which for a long time prevailed in both animal and vegetable histology. In this form of cell division the new wall commences as a ring-like projection from the inside of the wall of the mother cell, and gradually pushing farther into the cell, finally extends completely across it (Figs. 93, 94). In a division of this sort, in uninuclear cells, nuclear division precedes cell division, and the new wall is formed midway between the daughter nuclei (Fig. 93). In the multinuclear cells of the Thallophytes, on the other hand, although the nuclear division does not differ from that of uninuclear cells, cell division (Fig. 94) is altogether independent of nuclear division. And in multinuclear, unicellular Thallophytes, nuclear division is not followed by a cell division.

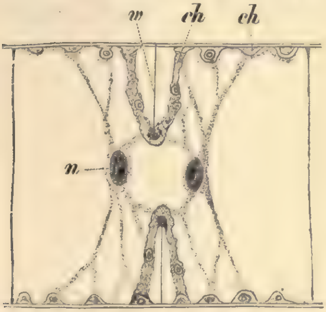


FIG. 93.—Cell of *Spirogyra* in division. *n*, One of the daughter nuclei; *w*, developing partition wall; *ch*, chloroplast pushed inward by the newly-forming wall. (× 230.)

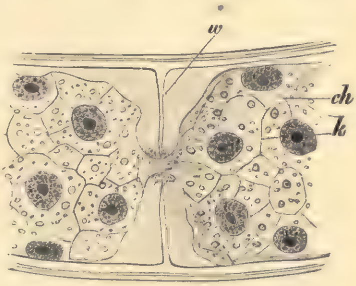


FIG. 94.—Portion of a dividing cell of *Cladophora fracta*. *w*, Newly-forming partition wall; *ch*, dividing chromatophore; *k*, nuclei. (× 600.)

The interdependence of nuclear and cell division in uninuclear cells is necessary to ensure a nucleus to each daughter cell. In multinuclear cells it is not essential that cell division should always be accompanied by nuclear division, as in any case a sufficient number of nuclei will be left to each daughter cell.

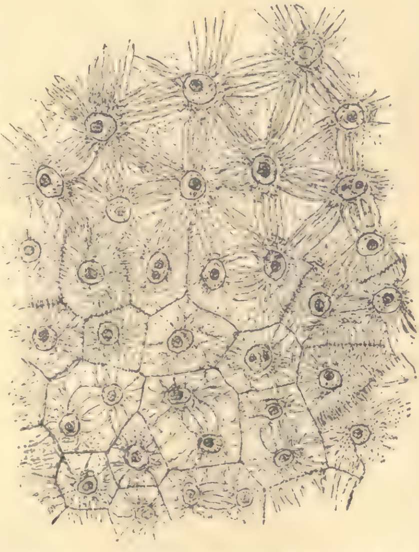


FIG. 95.—Portion of the peripheral protoplasm of the embryo-sac of *Reseda odorata*, showing the commencement of multicellular formation. The process progresses from above downwards. (× 240.)

Free Nuclear Division and Multicellular Formation.—The nuclear division in the multinuclear cells of the Thallophytes may serve as an example of free nuclear division, that is, of nuclear division unaccompanied by cell division. In plants with typical uninuclear cells, examples of free nuclear division also occur; although, in that case, the nuclear division is customarily followed by cell division. While the nuclei increase in number by repeated division, this process is not accompanied by a corresponding cell division. When, however, the number of nuclei is completed, the cytoplasm between the nuclei divides simultaneously into as many portions as there are nuclei. In this process we have an example of multicellular formation. This method of development is especially instructive in the embryo-sac of Phanerogams, a cell, often of remarkable size and rapid growth, in which the future embryo is developed. The nucleus of the rapidly growing embryo-sac divides, the two daughter nuclei again divide, their successors repeat the process, and so on, until at last thousands of nuclei are often formed. No cell division accompanies these repeated nuclear divisions, but the nuclei lie scattered throughout the peripheral, cytoplasmic lining of the embryo-sac. When the embryo-sac ceases to enlarge, the nuclei surround themselves with connecting strands, which then radiate from them in all directions (Fig. 95). Cell plates make their appearance in these connecting strands, and from them cell walls arise. In this manner the peripheral protoplasm of the embryo-sac divides, simultaneously, into as many cells as there are nuclei. Various intermediate stages between simultaneous, multicellular formation and successive cell division can often be observed in an embryo-sac. Where the embryo-sac is small and of slow growth, successive cell division takes place, so that multicellular formation may be regarded as but a shortened process of successive cell division, induced by an extremely rapid increase in the size of the cell.

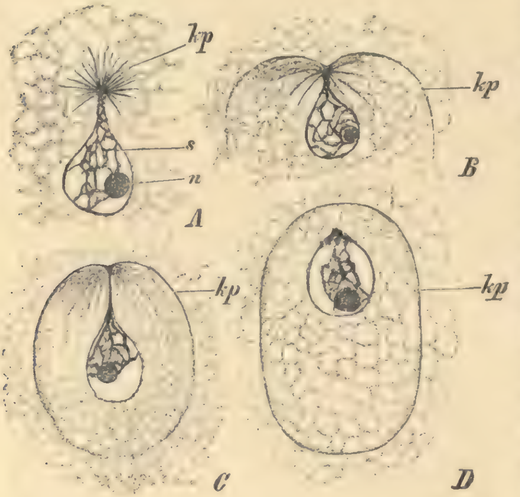


Fig. 96.—Successive stages of the delimitation of a spore in the ascus of *Erysiphe communis*. *A*, Before delimitation has begun; the fibrillar plasma (*kp*) radiates into the cytoplasm around; in *B* the fibrillar plasma has commenced to grow round the mass of cytoplasm; in *C* this process is complete, but the limiting layer produced by the fusion of radiations of the fibrillar plasma is still connected with the polar side of the nucleus; in *D* this kinoplasmatic connection between nucleus and limiting layer has disappeared; *s*, nuclear network; *n*, nucleolus. (After Harper, × 1500.)

Free Cell Formation.—Cells produced by this process differ conspicuously from those formed by the usual mode of cell division, in that the free nuclear division is followed by the formation of cells, which have no contact with each other, and in the formation of which the whole of the cytoplasm of the mother cell is not used up. This process can be seen in the developing embryo of the Gymnosperms, in

Ephedra, for example, and also in the formation of the spores of the Ascomycetes. A single nucleus is present to begin with in each ascus of the Ascomycetes. By successive divisions eight nuclei lying free in the cytoplasm are derived from this. A definite portion of cytoplasm around each of these nuclei becomes limited by a peripheral layer which then forms a cell wall. Thus eight separate spores arise (cf. Fig. 327). As the researches of Harper (86) have shown, the formation of the peripheral layer proceeds from a centrosome-like mass of kinoplasm which formed a pole of the spindle in the preceding nuclear division. The nucleus is drawn out towards this mass of kinoplasm. From the latter kinoplasmic radiations proceed which surround the spore as it becomes delimited, and finally fuse to form its peripheral layer (Fig. 96).

Cell-Budding.—This is simply a special variety of ordinary cell division, in which the cell is not divided in the middle, but, instead, pushes out a protuberance which, by constriction, becomes separated from the mother cell. This mode of cell multiplication is characteristic of the Yeast plant (Fig. 2, p. 11); and the spores, known as conidia, which are produced by numerous Fungi, have a similar origin (Fig. 353).

Conjugation (87).—A sexual cell is, with few exceptions, only able to continue its development after fusion with another sexual cell. The two cells so uniting are either alike, and in that case are called GAMETES, or unlike, and are then distinguished as EGG and SPERMATOZOID. The spermatozoid is the male, the egg the female sexual cell. The gametes may be motile (Fig. 97 *B*) or non-motile. The motile gametes frequently resemble the swarm-spores (Fig. 97 *A*) generated by the same parent for the purpose of asexual reproduction. As a rule, however, they are smaller than the swarm-spores, and have usually only half as many cilia. In the more highly specialised sexual cells the egg usually retains the structure of an embryonic cell, but the spermatozoid undergoes profound modifications. A cytoplasmic cell body, a nucleus, and the rudiments of chromatophores are always present in the egg. The spermatozoid (Fig. 98), on the other hand, becomes transformed, in the more extreme cases, into a spirally twisted body, provided with cilia, and exhibiting an apparently homogeneous structure. Only a knowledge of the history of its development, and the greatest care in hardening and staining, have rendered it possible to recognise the homology of the structure of such a spermatozoid with that of an embryonic cell. It has been shown that the hinder part of its spiral body corresponds to the cell nucleus (*k*), the anterior, together with the cilia, to the cytoplasm, especially the kinoplasm (*c*), and the vesicle (*b*), at the other extremity, to the sap cavity of a cell (88).

Motile male cells provided with cilia occur only in the Cryptogams and, as has been recently demonstrated (89), in some Gymnosperms (Cycadaceae, Ginkgo). In the Cryptogams the spermatozoids are set free from the sexual organs and require water for their dispersal. They reach the egg-cell, which usually remains in its place of origin, by swimming. In the Gymnosperms, which form motile spermatozoids, the latter are brought near to the ovum by means of the pollen tube developed from the pollen grain. In a similar way the non-motile male cells of the other Gymnosperms and the Angiosperms are conducted to the egg through the pollen tube (Fig. 99). In the union of the two sexual cells in the act of fertilisation, the egg nucleus (*ek*) and the sperm nucleus (*sk*) fuse and form the nucleus of the fertilised egg-cell. The cytoplasm of the male cell also commingles with that of the female cell, but the chromatophores of the embryo are derived from the egg-cell alone. When the spermatozoid, as in animals and in Thallophytes, is provided with a centrosome, this does not fuse with the centrosome belonging to the ovum. The centrosome of the fertilised egg-cell appears to be derived from that of the spermatozoid only.

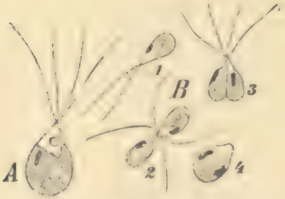


FIG. 97.—*A*, An asexual swarm-spore of *Ulothrix zonata*; *B*, 1, a gamete; 2 and 3, conjugating gametes; 4, zygote, formed by the fusion of two gametes. (× 500.)

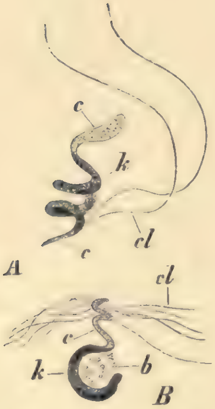


FIG. 98.—*A*, Spermatozoid of *Chara fragilis*; *B*, Spermatozoid of the Fern, *Onoclea struthiopteris*. (After SHAW.) The nucleus (*k*) is more deeply shaded; *c*, the cytoplasmic portion; *cl*, cilia which in *B* arise from the firmer edge of the spiral band; *b*, vesicle. (*A* × 540, *B* × 850.)

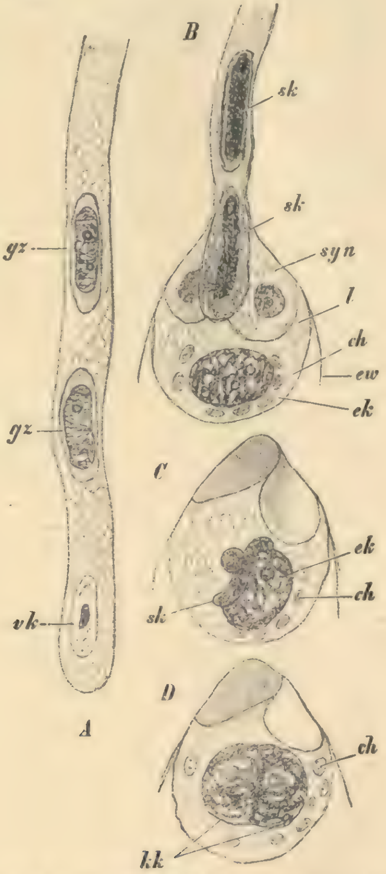


FIG. 99.—Fertilisation of a phanerogamic Angiosperm, somewhat diagrammatic. *A*, End of pollen tube; in it the generative cells *gz*, each of which contains a sperm nucleus; *vk*, the vegetative nucleus in process of dissolution. *B-D*, Egg in successive stages of fertilisation, —*B*, showing the generative cell with its sperm nucleus, *sk*, penetrating the egg; *syn*, the degenerating synergidæ; *C*, the union of sperm nucleus, *sk*, and egg nucleus, *ek*; *D*, the germ nucleus, *kk*, resulting from the fusion of the sperm and egg nuclei; *ch*, rudiments of chromatophores. (× about 500.)

The nuclei of the sexual cells always possess only the reduced number of chromosomes. By fertilisation the number becomes doubled, and after a shorter or longer period is again halved in the reduction division.

Although it is by fertilisation that the further development of the sexual products is made possible, there are exceptional cases in which a gamete or an egg forms an embryo without being fertilised. If development follows in this way from a gamete or egg with the reduced number of chromosomes the phenomenon is called PARTHENOGENESIS. On the other hand the reduction of the number of chromosomes may be suppressed in the development of the egg so that the full number necessary for further development is already present in it. In this case its development is not true parthenogenesis but a vegetative production of an embryo, which has come about through loss of sexuality and falls under the conception of APOGAMY (⁹⁰). The cases of production of embryos from unfertilised eggs among the higher plants belong to the latter category: this is known in *Antennaria alpina* (⁹¹), *Alchemilla* (⁹²), *Thalictrum purpurascens* (⁹³), *Taraxacum* (⁹⁴), *Hieracia* (⁹⁵). In lower plants, in some Fungi, *e.g.* Saprolegnieae, and in one of the Characeae (*Chara crinita*) (⁹⁶) true parthenogenesis is found. In *Marsilia* (⁹⁷), one of the Hydropterideae, the segmentation and further development of unfertilised eggs has also been observed.

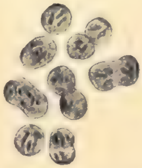


FIG. 100.—Chlorophyll grains from the leaf of *Funaria hygrometrica*, resting, and in process of division. Small included starch grains are present in the grains. (× 540.)

Multiplication of the Chromatophores.—This is accomplished by a direct division, as a result of which, by a process of constriction, a chromatophore becomes divided into nearly equal halves. The stages of this division may best be observed in the chloroplasts (Fig. 100).

B. Cell Fusions

The connection of the living protoplasts with one another is less complete in plants than in the animal body. This is evident from the existence of the cell wall which surrounds the vegetable protoplast. Recent researches have, however, shown (⁹⁸) that the protoplasts of the plant are united together by extremely fine cytoplasmic filaments, which proceed from the boundary layer of the cytoplasm. Such filaments are mostly confined to the pit-membrane (Fig. 101), but may also penetrate the whole thickness of the cell wall (Fig. 102). The existence of these connecting filaments of living substance between the protoplasts confers an organic unity on the whole body of the plant.

The members which make up the sieve-vessels, or, as they are commonly called, the sieve-tubes, are united by thicker strands of cytoplasm, which facilitate the transfer of substances through the tube. The transverse walls traversed by these strands of cytoplasm have been referred to above (p. 67) as sieve-plates. The pores attain their greatest diameter in some Angiosperms (Fig. 103). It is worthy of special note that, despite the fact that the nuclei of the sieve-tube segments disintegrate, the cytoplasm, which lines the wall, remains alive. The walls of sieve-tubes are always unlignified. Their sap-cavities contain a watery, and more or less dilute, solution of albuminous substances, and small starch grains are also present in most cases. As a rule, the sieve-tubes remain functional only through one or a few vegetative periods. Before their activity ceases the sieve-plates become covered (Fig. 103 *C*) with highly refractive callus (p. 69).

A more complete fusion of protoplasts is found in the formation of laticiferous vessels. These have the same structure and contents as latex cells (p. 72). Their occurrence, like that of latex cells, is limited to a few distinct plant families, such as the Papaveraceae, of which the Poppy (*Papaver*) or Celandine (*Chelidonium*), with its characteristic orange-coloured "sap," are familiar examples, or the Compositae, of which in particular the Lettuce (*Lactuca*) may be cited. Latex vessels are distinguished from latex cells only by the method of their development, which has resulted from the fusion of rows of elongated cells, the separating transverse walls of which have become more or less completely absorbed. Such vessels as a rule possess lateral branches, which, on meeting with one another, fuse by the absorption of their end walls (Fig. 104). The mucilage tubes ([61]) which are found in many Monocotyledons present points of resemblance to the laticiferous vessels. Their

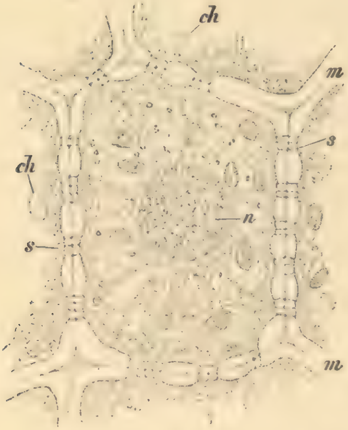


FIG. 101.—A cell from the cortex of the Mistletoe (*Viscum album*); the protoplast has been properly fixed and stained and the wall (*m*) swollen. The pit-membranes (*s*) are traversed by connecting threads; *ch*, chloroplasts; *n*, nucleus. (× 1000.)

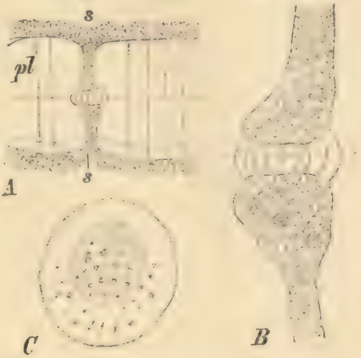


FIG. 102.—*A*, A swollen portion of cell wall from the endosperm of the Vegetable Ivory Palm (*Phytelephas macrocarpa*). At *s*, *s*, simple pits filled with cytoplasm; in the intervening pit-membrane are fine connecting threads; *pl*, other threads traversing the whole thickness of the wall. (× 375.) *B*, The contents of two opposed pits and the connecting threads of the pit-membrane. (× 1500). *C*, The opening of a pit and the connecting threads of the pit-membrane viewed from the surface. (× 1500.)

mucilaginous sap contains albumen, starch, glucose, and tannins in addition to inorganic compounds.

A cell fusion also takes place in the formation of VESSELS or TRACHEÆ, but it should not be considered as a union between living cell bodies, but merely as one between cell cavities. The mature vessels are dead tubes serving for water conduction. They are formed from rows of cells, the lateral walls of which are peculiarly marked by spiral or reticulate thickenings, or, as is more frequently the case, by bordered pits, while the transverse walls become more or less completely absorbed. In cases where the transverse walls are at right angles to the side walls, they usually become perforated by a single large round opening while the remains of the wall forms a thickening ring (Fig. 73 *C*). When the transverse walls are oblique, they are perforated by several openings, between which portions of the wall remain, like rungs of a ladder (Fig. 105 *q*). According to the mode of their wall thickening, vessels are distinguished as SPIRAL, RETICULATE, or PITTED. When the transversely elongated pits of a vessel are arranged in more or less parallel rows (Fig. 105), it is called a SCALARIFORM VESSEL. The thickening of the vessel walls is always lignified. The living contents of the cells, after the perforation of the transverse walls, become completely absorbed, and the fully formed vessels or tracheæ contain only water and a limited amount of air.

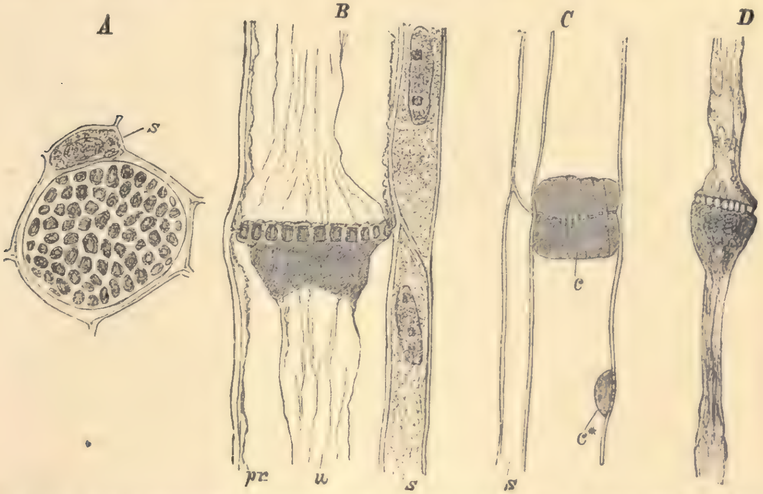


FIG. 103.—Parts of sieve-tubes of *Cucurbita Pepo*, hardened in alcohol. *A*, Surface view of a sieve-plate; *B*, *C*, longitudinal sections, showing segments of sieve-tubes; *D*, contents of two sieve-tube segments, after treatment with sulphuric acid; *s*, companion cells; *u*, albuminous contents: *pr*, peripheral cytoplasm; *c*, callus plate; *c**, small, lateral sieve-pit, with callus plate. (× 540.)

There is no difference between vasiform tracheides and vessels other than that the former are single elongated cells, and the latter fused cell rows. Generally speaking, tracheides are formed in parts of plants still in process of elongation, vessels in parts where growth in length has already ceased. True vessels make their first appearance in some of the Ferns, for instance, in the common Bracken (*Pteris aquilina*). In the main, despite the name Vascular Cryptogams, Ferns have only vasiform tracheids. Even in the Gymnosperms the Gnetaceae are the only family regularly provided with vessels. It is in the Angiosperms that vessels first become of frequent occurrence. Vessels are not of an unlimited length. A few plants, however, such as the Oak, and especially climbing woody plants, or Lianes, have vessels several metres long; but, as a rule, their length is not more than a metre, and in plants the woody portion of which conducts water only by vessels, the vessels have an average length of only ten centimetres. The length of an individual vessel is defined by the presence of transverse walls, which are not perforated but bear bordered pits.

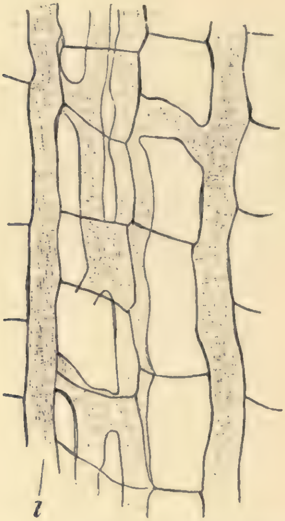


Fig. 104.—Tangential section through the periphery of the stem of *Scorzonera hispanica*, showing reticulately united latex vessels. (× 240.)

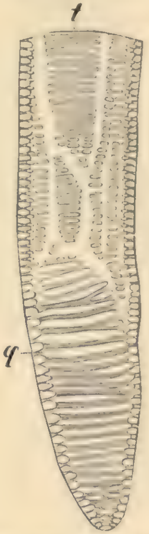


Fig. 105.—Lower third of a scalariform vessel from the rhizome of the common Bracken Fern, *Pteris aquilina*. *t*, Transversely elongated pits in the lateral walls; *q*, scalariform perforations of the terminal wall. (After De Bary, × 95.)

A similar fusion to that seen above to occur in the formation of laticiferous vessels is also met with in fungal hyphæ; by an absorption of a part of the wall where two branches come into contact, their protoplasmic contents unite. A still more complete fusion is exhibited by the naked amœbæ of a Myxomycete in forming the plasmodium

(p. 56). The fusion of the sexual cells in the process of fertilisation possesses special characteristics which place the process in a distinct category.

Tissues (99)

Origin and General Properties of Tissues.—A continuous aggregation of cells in intimate union is called a tissue. The origin of vegetable tissues is, in general, attributable to cell division. It is only in the Fungi and Siphoneae that a tissue arises through the interweaving of tubular cells or cell filaments (Fig. 106). In such cases, where the filaments are so closely interwoven as to form a compact mass of cells, the tissue thus formed has the same appearance as the tissues of higher plants (Fig. 107).

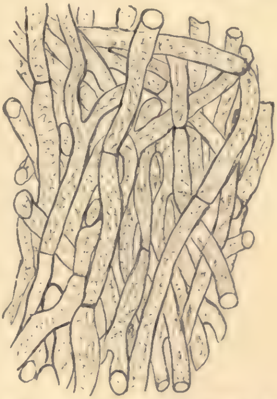


FIG. 106.—Longitudinal section of the stalk of the fructification of *Boletus edulis*. (× 300.)

The mutual interdependence of the cells of a tissue is manifested both by the conjunction of their pits (Figs. 66, 70, 71), and by the general similarity of their wall thickenings.

The cells in a tissue may either fit closely together (Fig. 70), leaving no openings or spaces, or so-called INTERCELLULAR SPACES may be left between the individual cells. Where cell filaments are interwoven into a tissue, the intercellular spaces are represented by the openings left between the loosely-woven filaments (Fig. 106). In tissues resulting from cell division the intercellular spaces arise subsequently, as the partition wall between two cells formed by cell division is originally a simple membrane.

Such a partition wall may ultimately split and so give rise to intercellular spaces, but this only occurs after it has been thickened. The cause of such splitting is to be found in the hydrostatic pressure existing within the cells, and their consequent tendency to assume a spherical shape. The formation of intercellular spaces commences, therefore, at the cell corners, where the primary wall, consisting of pectinose material, becomes swollen.

The simplest and at the same time most frequent intercellular spaces are triangular or quadrangular in outline, as seen in cross-section (Figs. 66 *i*, 74 *i*). In cases where special portions of adjoining cells are in extremely energetic growth, intercellular chambers and passages, of more or less irregular shape, may be formed between them. If the growth of adjoining cells is very unequal, it may lead to a complete separation of their cell walls; or the cells, or even a whole system of tissues, may be stretched and torn apart. It is by such a process that hollow stems are formed. Intercellular spaces arising from a splitting of adjoining cell walls are termed SCHIZOGENIC; those formed by tearing or dissolution of the cells themselves are called LYSIGENIC INTERCELLULAR spaces. In many cases intercellular spaces that begin as schizogenic are increased in size by destruction of surrounding cells. Most intercellular spaces contain only air, although in special instances they may contain water or excreted products, such as gum, mucilage, resin, or ethereal oils, and in other still rarer cases latex. Schizogenic intercellular spaces are usually filled with air, and form the ventilating system of the plants, while the lysigenic spaces often contain either water or secretion products.

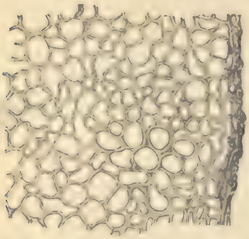


FIG. 107.—Transverse section of the sclerotium of *Claviceps purpurea*. (× 300.)

Of the schizogenic intercellular spaces, those filled with ethereal oils or resin, on account of their frequency, should be particularly noticed. Short cavities and longer passages, or ducts, containing ethereal oils, are to be found in the stems, roots, and leaves of numerous plant families. The Umbelliferae are especially rich in these, and the oil-ducts form the characteristic markings (vittæ) on their fruits. The Conifers are especially characterised by resin-ducts (Fig. 141 A, *h*), which, even during their formation by the separation of the cell walls, seem to fill with the excretion from the cells. The enlargement of such intercellular spaces is accompanied by a division of the surrounding cells, the number of which is thus correspondingly increased. The cells themselves remain thin-walled, and in close contact laterally, but bulge out somewhat into the ducts. Lysigenic intercellular spaces, acting as receptacles for secretions, have the appearance of irregular cavities in the tissue. Where they contain oil or resin, they develop from a group of cells in which these substances appear in the form of drops. The cell group then becomes disorganised by the gradual absorption of the cell walls. In this way are formed the receptacles filled with ethereal oils, in the Orange and Lemon. The formation of the so-called resin-galls, in the case of coniferous trees, is preceded by the formation of abnormal tissues, which afterwards become converted into resin. Such was also the origin of amber, which is the fossil resin of the Amber-fir (*Picea succinifera*). The formation of gum in lysigenic gum cavities is due to the modification of the cell walls, and either normal tissues participate in this process, as in the case of the gum-arabic of the Acacia, or abnormal tissues are first developed and then transformed into gum, as, for example, the gum on Cherry trees. Latex does not occur in lysigenic intercellular spaces.

The separating walls resulting from cell division are simple lamellæ. In tissues which have arisen by cell division these lamellæ are common to the cells they separate. That part of the partition wall between two cells which stands out so distinctly in a cross-section does not consist of the original primary cell wall alone. It is made up of both the primary wall and the primary thickening layers. The former is called the MIDDLE LAMELLA (Figs. 66 *m*, 70 *m*). In soft tissues the middle lamella, according to DEVAUX (100), is composed for the most part of pectic substances; in woody and corky tissues it is also lignified. By boiling soft tissues in water, the cells may often be easily isolated through the consequent swelling and dissolution of the middle lamella. In ripe fruit, an isolation of the cells frequently takes place spontaneously, through the dissolution of the middle lamella. A lignified middle lamella, on the other hand, seems able to withstand more effectually the action of oxidising agents. Consequently, it is possible, by subjecting a section of pine-wood to the action of SCHULZE's MACERATING MIXTURE (potassium chlorate and nitric acid), and subsequently treating with concentrated sulphuric acid, to remove all secondary and tertiary thickening layers, so that only the middle lamellæ remain as a delicate network. If the macerating process be continued for a longer time, without the subsequent treatment with sulphuric acid, the middle lamellæ become finally dissolved. The thickening layer will then be left free from all lignification. SCHULZE's macerating method may accordingly be employed to isolate the elements of lignified tissues. The peculiar relation of the middle lamella towards chemical reagents gave rise at one time to the presumption of a special intercellular substance which, like a glue, bound together the cells of a vegetable tissue. The supplementary deposition of pectic compounds in the middle lamellæ (p. 69) frequently gives rise to the formation of rod-like protuberances and excrescences, which project into the intercellular spaces, or these spaces may be filled up by the formation of gussets (Fig. 70 *C*, *m**).

Kinds of Tissue.—The mature tissues of the plant may be divided into two groups, PARENCHYMA and PROSENCHYMA, between which, however, no sharp distinction can be made. A typically developed parenchymatous tissue is one in which the thin-walled cells are equally expanded in all directions, and possess a layer of protoplasm lining the wall, and other cell contents. Typical prosenchymatous tissue, on the other hand, consists of thick-walled, elongated cells, either in the form of fibres or spindle-shaped cells, with interlocking, pointed ends, and with little or no protoplasmic contents. A parenchymatous tissue, in which the cells are thick-walled and elongated, resembles prosenchyma, but may be distinguished from it by the absence of pointed cell terminations, and especially by the greater abundance of protoplasm. Thin-walled prosenchyma is not, on the other hand, necessarily lacking in protoplasm, but is characterised by its pointed and interlocking cells.

An undifferentiated tissue, the cells of which are still capable of division, is termed embryonic tissue, or MERISTEM. The meristem of embryonic rudiments and of the growing point is called PROMERISTEM, and all meristematic tissue which can be shown to have been derived directly from such promeristem is termed PRIMARY. A primary meristem may still retain its meristematic character in the midst of a mature tissue. Fully differentiated tissue is designated PERMANENT tissue, or somatic tissue, in contrast to meristematic tissue. At times, permanent tissue may again become capable of division, and thus give rise to a SECONDARY MERISTEM.

A mass of tissue so united in the body of a plant as to form a higher histological unit constitutes a tissue system. In the more highly organised plants three such systems may be distinguished—the TEGUMENTARY SYSTEM, the VASCULAR BUNDLE SYSTEM, and the FUNDAMENTAL TISSUE SYSTEM.

The tissues which make up the different tissue systems are distinguished as PRIMARY and SECONDARY, according to their origin. The primary are those which are derived from the promeristem and primary meristems before growth in length has been completed; the secondary are those which owe their origin to the primary or secondary meristems after growth in length is finished.

The primary constituents of the tissue systems will be considered first.

A. The Primary Tissues

The Tegumentary System.—In the Pteridophytes and Phanerogams the plant body is covered by a distinct outer layer of cells or EPIDERMIS; this is wanting in plants of the lower groups. A typically developed epidermis consists of one layer of cells (Fig. 74 *e*), the outer walls of which on the free surfaces of the plant are more strongly thickened. This is especially the case in all aerial parts of plants adapted for a long life, but on the more perishable parts of a plant, such as the floral leaves, or on subterranean parts such as the roots, the cells of the epidermal layer are generally thin-walled or only slightly thickened. For such reasons the epidermis of the root was formerly termed the epiblem. Even when the external walls of the epidermal cells are considerably thickened, the side walls, at least in part, remain unthickened. The external walls are also more or less cuticularised, while their outermost layer, which is more decidedly cuticularised and capable of withstanding even the action of concentrated sulphuric acid, extends as a CUTICLE continuously over the surface of the epidermis. This cuticle appears to be always wanting from the epidermis of roots ([101]). The cuticle has its origin in the primary walls of the younger epidermal cells, which, during the increase in size of the plant, grow in area, and at the same time are strengthened by the deposition of cutin. The cuticle of leaves in the tropics is often specially smooth and shining. It reflects a portion of the sunlight, giving rise to the sparkling appearance characteristic of tropical foliage, and serves to protect the plant from too strong insolation. The cuticle frequently becomes folded, and so assumes a striated appearance (Fig. 114). By the thickening and the cutinisation of their outer walls the mechanical rigidity of the epidermal cells is increased, and the loss of water by transpiration is lessened. Plants in dry climates, or so situated that, for any reason, transpiration from their outer surfaces must be diminished, are characterised by the greatly thickened and cuticularised walls of their epidermal cells. In some of the Gramineae, Equisetaceae, and many other plants, the cell walls of the epidermis are silicified. In the Equisetaceae the impregnation with silica is so considerable that these plants are used for polishing. Heating, even to redness, does not destroy the structure of such silicified epidermal cells.

Deposits of wax are also present in the cutinised layers of the epidermis, and consequently water will flow off the epidermis without wetting it. The wax is sometimes spread over the surface of the cuticle as a wax covering. This is the case in most fruits, where, as is so noticeable on plums, it forms the so-called bloom.

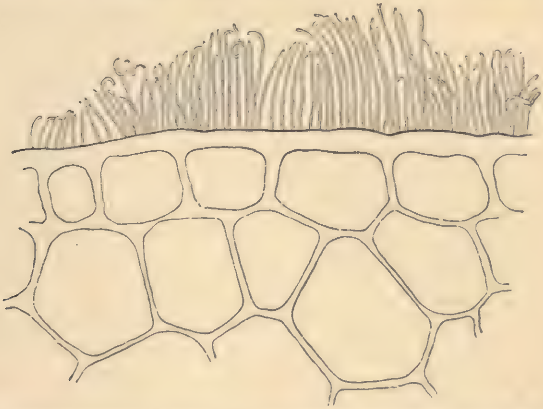


FIG. 108.—Transverse section of a node of the sugar-cane, *Saccharum officinarum*, showing wax incrustation in the form of small rods. (× 540.)

The wax coverings may consist of grains, small rods (Fig. 108), or crusts.

The wax deposits attain their greatest thickness on the leaves of some of the Palms; on the Peruvian Wax Palm, *Ceroxylon andicola*, the wax covering is more than 5 mm. thick. This wax, as well as that obtained from the fruit of *Myrica cerifera*, is known as vegetable wax, and possesses an economic value. The wax incrustations may be melted by heat; they are soluble in ether and in hot alcohol. In many cases, in place of the wax coverings, small grains and scales of a fatty substance, which is soluble even in cold alcohol, are excreted. The dusty coverings thus formed appear either mealy white or golden yellow, and are the cause of the striking appearance of the Gold and Silver Ferns, especially in species of *Gymnogramme*.

In many cases, slimy or sticky excretions are produced between the thickening layers of the epidermis and the cuticle; these press up the latter and finally burst it. Such excreting surfaces often occur on bud-scales. Sticky zones are frequently formed on stems, as in the case of *Lychnis viscaria* and other Sileneae, as a means of protection to the flowers higher on the stem from undesirable visitors. Small creeping insects, which would otherwise rob the flowers of their honey, seem as little able to pass beyond such a sticky zone, as other larger animals to surmount the rings of tar often placed around the trunks of fruit trees for a similar protective purpose. Excreting epidermal surfaces form also the nectaries of flowers, which by means of their sweet secretions attract such animals, generally insects, as are instrumental in their pollination.

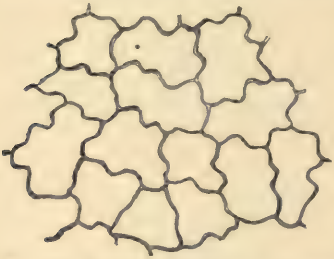


FIG. 109.—Surface view of the epidermis from the upper side of a leaf of *Mercurialis perennis*. (× 300.)

The cells of the epidermis are in uninterrupted contact with each other, and as a rule have undulating side walls (Fig. 109). The protoplasm of epidermal cells generally appears to be reduced to a thin, peripheral layer, and the sap cavities filled with a colourless or coloured sap. Around their nuclei cluster the colourless rudiments of the chromatophores, showing that, although exposed to the light, their further development into chloroplasts may cease in cells not destined to take part in the assimilatory processes. Such epidermal cells with undeveloped chromatophores, besides acting as an external protection, serve as water-reservoirs; their side walls, by means of folds in the unthickened parts, can expand and collapse as a bellows, according to the variations in their supply of water. In plants which grow in shade chlorophyll is usually present in the epidermal cells.

The external walls of the epidermal cells of this upper surface of foliage leaves not uncommonly project or exhibit a lens-shaped thickening in the middle (Fig. 75); this arrangement serves to concentrate the rays of light. The refractivity of the lens-shaped thickening is rendered greater by pectinisation, cutinisation, silicification, or waxy secretions. In the cases where the optical apparatus is formed by a bulging of the uniformly thickened wall, the cell-sap containing much tannin serves as the refractive medium (102).

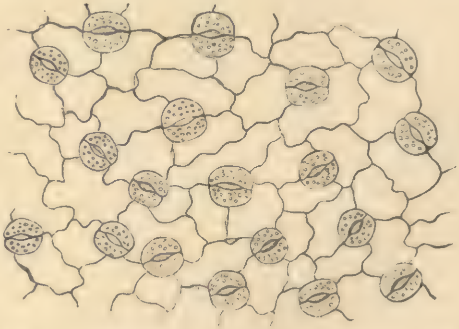


FIG. 110.—Epidermis with stomata from the lower surface of the leaf of *Helleborus niger*. (× 120.)

The formation of stomata (103) in the epidermis is characteristic of all parts of the more highly-developed plants which are exposed to the air. Each stoma consists of an intercellular passage perforating the epidermis and bounded by two elliptical epidermal cells, termed

GUARD-CELLS (Figs. 110, 111 *A*). The guard-cells always contain chloroplasts, and are also characterised by their peculiarly thickened walls. These, as is best seen in transverse sections, form ridge-like protuberances projecting above and below from the sides of the guard-cells adjoining the air-passage (Fig. 111 *B*). Midway between the projecting ridges, on the other hand, the walls of the guard-cells remain unthickened (Fig. 112).

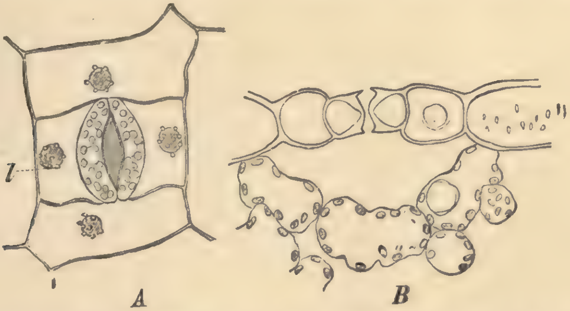


FIG. 111.—Epidermis from the under side of a leaf of *Tradescantia virginica*. *A*, In surface view; *B*, in transverse section; *l*, colourless rudiments of chromatophores surrounding the nucleus. (× 240.)

The unthickened parts of the walls of guard-cells jut out into the pore (Figs. 111 *B*, 112), and thus facilitate its closing. In addition, the external thickened walls of the two adjacent epidermal cells become, in some cases, suddenly thin on approaching the guard-cells. By this means a hinge-like connection is formed which renders the guard-cells more or less independent of the other epidermal cells. At other times the same result is accomplished by raising the stomata above the epidermis, or, more frequently, by sinking them below the less thickened epidermal

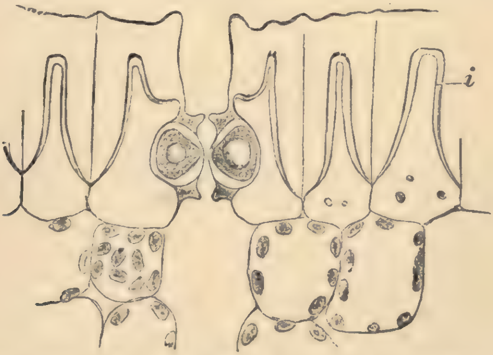


FIG. 112.—Transverse section of the epidermis of *Aloe nigricans*. *i*, Inner, uncutinised thickening layer. (× 240.)

walls. The elevation serves to increase the evaporation, and is on this account met with in Ferns which grow in damp situations. The depression diminishes the transpiration by creating a still atmosphere above the guard-cells. On this account it is met with in plants of dry regions (xerophytes). Frequently the epidermal cells adjoining the guard-cells are less thickened or lower than the other cells of the epidermis (Fig. 111). Such special epidermal cells are called SUBSIDIARY CELLS, and have the same use as the hinge joint mentioned above.

The stomata are formed by the division of a young epidermal cell into two cells of unequal size, one of which, the smaller and more abundantly supplied with protoplasm, becomes the stoma mother-cell; while the larger, containing less protoplasm, usually forms an ordinary epidermal cell. The stoma mother-cell becomes elliptical in outline and divides again, by a vertical wall, into the two guard-cells, between which, by a splitting of the wall, the intercellular passage (pore) is formed. Before the formation of the definitive stoma mother-cell, successive divisions of the young epidermal cell often occur; in such cases the finally developed stoma is generally surrounded by subsidiary cells.

Stomata are chiefly developed on the green parts of plants, but are sometimes found even on the coloured floral leaves. They are naturally found in greatest numbers on the leaves, as it is there that they are most needed to facilitate the interchange of gases in the processes of assimilation. In dorsiventral leaves the stomata occur, for the most part, if not exclusively, on the under surface, and average about 100 to the square millimetre, although in some plants their number may reach 700. Leaves which are alike on both sides have their stomata equally distributed on the two surfaces. Floating leaves of aquatic plants have stomata only on the side exposed to the air. In some cases, as in the Oleander (*Nerium Oleander*), numerous stomata are situated together in pit-like depressions of the under surfaces of the leaves. In the tissue directly under each stoma there is always a large intercellular space, termed the RESPIRATORY CAVITY (Fig. 111 *B*), which is in direct communication with the other intercellular spaces extending throughout the leaf tissue. In plants grown in abundance of moisture, these intercellular spaces are usually larger than in the case of plants growing in drier situations.

In contrast to the stomata, which as air-pores serve for the interchange of gases, a few plants also possess WATER-STOMATA or WATER-PORES, situated at the ends of the veins or nerves of the leaves. These pores serve as organs for the discharge of water or watery solutions. Calcium carbonate, in solution, is frequently excreted in this way, and in many species of *Saxifraga* it forms white scales on the margins of the leaves. Although water-pores may often be found at the apices and tips of the marginal teeth of young leaves, they seem to dry up as the leaves become more mature. The guard-cells of water-stomata usually lose their living contents early, and thus the passage between them remains continually open. The water-stomata (Fig. 113) are always larger than the air-stomata.

Although submerged leaves of aquatic plants are devoid of air-stomata, water-stomata often occur on them.

Hairs or TRICHOMES and EMERGENCES are characteristic of the tegumentary system. The cells of the hairs may retain their living contents, or die and become filled with air; in the latter case the hairs appear white. The simplest form of hairs are the PAPILLÆ, which are merely epidermal cells, the external walls of which have protruded in a conical form. Papillæ are often developed on the petals of flowers, and are the cause of their velvety appearance (Fig. 114). Longer hairs, such as the root hairs (Fig. 170 *r*), are also prolongations of single epidermal cells; these are characteristic of definite regions of the root, and only a limited portion of the outer wall of the epidermal cell protrudes as a hair. The woolly hairs found in young buds are generally similarly prolonged epidermal cells which, as a protective covering, surround the young growing tissues and sometimes remain on fully developed parts of plants to protect them against too rapid evaporation and direct insolation. The hairs developed from some of the epidermal cells of the seed coats of various species of *Gossypium* attain an unusual length, and supply the cotton of commerce (Fig. 115). These cotton hairs are sometimes 6 cm. long, and in their fully developed state contain only air; their cell walls are thicker than those of ordinary hairs, and covered with a delicate cuticle. They are usually somewhat flattened and at the same time twisted; and are wider in the middle than at either end. Only a certain number of the epidermal cells of the seed grow out as cotton hairs (Fig. 115 B_1). BRISTLES are short, pointed hairs, in the thickened cell walls of which calcium carbonate or silica has been deposited (Fig. 116, below, to the right).

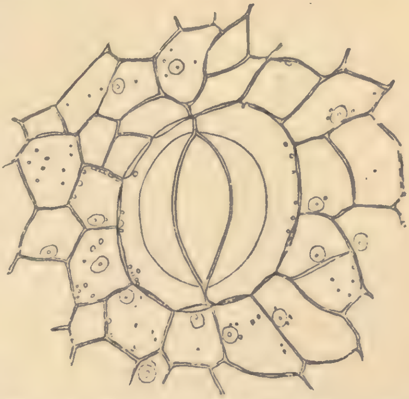


FIG. 113.—Water-pore from the margin of a leaf of *Tropaeolum majus*, with surrounding epidermal cells. (× 240.)

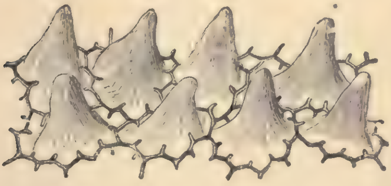


FIG. 114.—Surface of the upper epidermis of a petal of *Viola tricolor*, showing ridge-like projections from the lateral walls, and protruding papillae. (× 250.)

The STINGING HAIRS (Fig. 116), such as those of Nettles (*Urtica*) and of the Loasaceae, are special forms of bristles, and arise as prolongations of single epidermal cells. These, however, swell in the course of their development, and becoming surrounded by adjoining epidermal cells present the appearance of being set in sockets; while, at the same time, by the multiplication of the cells

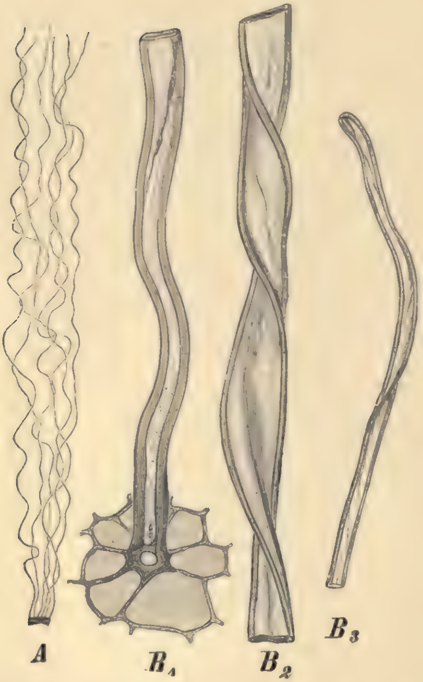


Fig. 115.—Seed-hairs of the cotton, *Gossypium herbaceum*. *A*, Part of seed-coat with hairs (× 8) B_1 insertion and lower part, B_2 middle part, and B_3 upper part, of a hair. (× 300.)

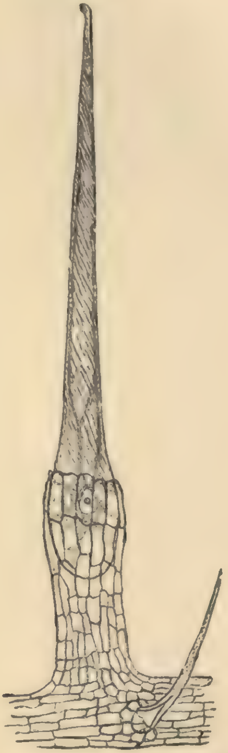


Fig. 116.—Stinging hair of *Urtica dioica*, with a portion of the epidermis, and, to the right, a small bristle. (× 60.)

in the tissue at their base, the whole hair becomes elevated on a column-like protuberance. The hair tapers towards the apex and terminates, somewhat obliquely, in a small head, just below which the wall of the hair remains unthickened. As the wall of the hair is silicified at the end and calcified for the rest of its length, the whole hair is therefore extremely stiff. Such hairs furnish a means of defence against animals. The heads break off at the slightest touch, and the hairs piercing the skin pour out their poisonous contents, which, especially in the case of some tropical nettles, may cause severe inflammation.

The cells surrounding the base of a hair are often arranged in a ring or in radiating lines, or are otherwise different from the surrounding epidermal cells. Such cells may be called subsidiary cells to the hairs.

UNICELLULAR HAIRS, such as we have so far considered, may terminate in well-defined heads resulting from the swelling of their tips, or their side walls may develop irregular excrescences; on the other hand, they may remain short and expanded like a balloon, or remain close to the surface of the epidermis as spindle-shaped or stellate hairs. MULTICELLULAR HAIRS may be merely simple rows of similar cells, as the hairs on the stamens of *Tradescantia* (Fig. 60); or their terminal cells may become swollen into globular heads (Fig. 117), like those on the Chinese Primrose (*Primula sinensis*); or an epidermis may be covered with disc-, star-, or bowl-shaped hairs (Fig. 118). Sometimes the hairs become variously branched, lose their living contents, and form a silky or woolly protective covering similar to that formed by unicellular hairs. In special cases, as in the scale hairs of Ferns, they may even have the shape of a small leaf.

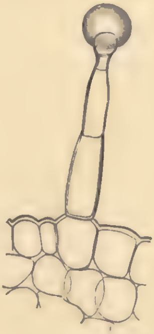


FIG. 117.—Glandular hair from the petiole of *Primula sinensis*. (After DE BARY, × 142.)

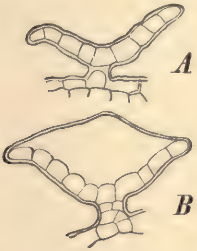


FIG. 118.—Glandular scale from the female inflorescence of the Hop, *Humulus Lupulus*, in vertical section. *A*, before, *B*, after the cuticle has become distended by the excretion. In *B* the excretion has been removed by alcohol. (After DE BARY, × 142.)

EMERGENCES, unlike hairs, are not formed solely by epidermal cells, but a number of cells, lying more or less deeply in the sub-epidermal tissues, also take part in their formation. Thus, for example, while only a few rows of sub-epidermal cells enter into the formation of the emergences (Fig. 119) on the margins of the stipules of the Pansy (*Viola tricolor*), much deeper-lying tissue participates in the development of the emergences which, as PRICKLES, serve in the case of Roses as a means of protection, and at the same time are of assistance in climbing. The thick emergences, which spring from the roots of the Podostemaceae, and serve to attach them to rocks, are parenchymatous throughout, but vascular bundles may be included within emergences, as is well shown in the club-shaped digestive glands or tentacles (Fig. 120) on the leaves of the Sundew (*Drosera*). Some emergences resemble in structure certain of the metamorphosed members of the plant body described in the preceding chapter; the resemblance between prickles and thorns, and between haptera and lateral roots will serve as examples. They are not, however, to be traced back in origin to such members (p. 50).

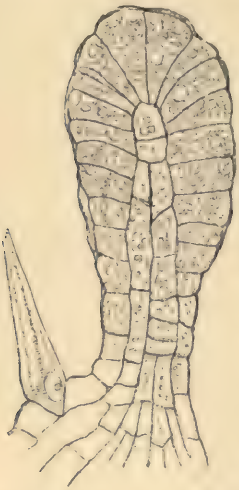


FIG. 119.—Glandular colleter from a stipule of *Viola tricolor*, showing also a unicellular hair. (× 240.)

Both hairs and emergences frequently act as secreting organs, and are then termed GLANDS. In many cases they are concerned with the active exudation, and at times also the absorption of water. They then belong to the class of organs designated HYDATHODES (104) by HABERLANDT. Other glandular hairs excrete a resinous substance. The hairs of *Primula sinensis* (Fig. 117) are in reality such glands, in which the cuticle of the terminal globular head is pressed away from the cell wall by the resinous matter excreted from the hair, until finally the bulging cuticle is ruptured and the resinous secretion exudes. The hairs of this and other species of *Primula* (especially *P. obconica*) are capable of exciting inflammation in the skin of those handling them (106). Only some persons are susceptible to the effect. The similar but more complicated glandular hairs of Hops (Fig. 118) produce a secretion called LUPULIN, to which beer owes its bitter taste and distinctive aroma. The secretion is set free by the bursting of the cuticle, the latter having been previously raised up from the underlying cell wall as a continuous membrane (Fig. 118 *B*). Hairs and emergences with abundant protoplasmic contents occur on irritable stamens, perianth leaves, and pulvini, and, as HABERLANDT (105) showed, act as tactile papillæ, hairs, or bristles in the reception of stimuli. In other cases they are not themselves irritable, but serve to conduct a stimulus mechanically towards the irritable tissue.

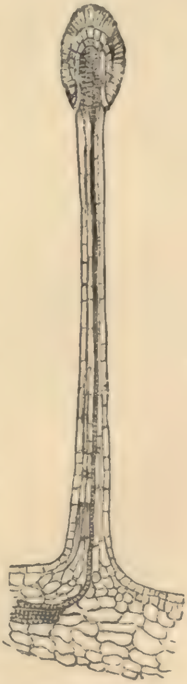


FIG. 120.—Digestive gland from *Drosera rotundifolia*. (× 60.)

The mucilaginous matter produced in young buds by the mucilage papillæ or COLLETERS results from the partial dissolution of the cell wall under the cuticle. After the mucilaginous secretion has been discharged by the ultimate rupture of the cuticle, another new cuticle forms over the cell wall, and the process is again repeated. The colleters are special forms of hairy structures, and are often developed in buds to protect the young organs from drying, by means of the mucilaginous modification of their cell walls. Where the dissolution of the cell wall is accompanied by secretions from the underlying cells, the colleters assume rather the character of glandular hairs. Such GLANDULAR COLLETERS are common in the winter buds of trees ; in the Horse-chestnut (*Aesculus Hippocastanum*), for example, the bud-scales of the winter buds are stuck together by a mixture of gum and resin, which has exuded from colleters of this nature. The glandular hairs of the Pansy (Fig. 119) act in a similar manner. The emergences on the leaves of the Sundew (*Drosera*), described as digestive glands (Fig. 120), discharge glistening drops of mucilaginous matter, not under the cuticle, but from the free surface of the glands at the ends of the tentacles. Small animals are caught by means of these sticky excretions, and are afterwards digested by the plant. The nectaries also often excrete sugary solutions directly from their surfaces. In flowers these serve to attract insects, which effect pollination, while on other parts of the plants they are known in certain cases to attract ants, which protect the plant. The osmotically active substances in the nectar are in the first instance derived by transformation of the outer cell walls, or are secreted by the cells. The presence of these substances on the surface of the nectary attracts water from the tissue beneath, and thus leads to the continued formation of the nectar.

In some of the Piperaceae and Begoniaceae, and in some species of *Ficus*, the epidermis is composed of several layers ; but this is a comparatively rare occurrence. Such a many-layered epidermis results from a division of the young epidermal cells parallel to their external surface. The epidermis of *Ficus elastica* (Fig. 76) has three layers, and serves as a reservoir for accumulating water. The cystoliths of *Ficus elastica*, already referred to (p. 68), occur in single swollen epidermal cells. A many-layered root epidermis is also met with, as in species of *Asparagus*, *Crinum* and *Lycoris* ([107]). The many-layered epidermis of the aerial roots of many Orchids, and of various Aroids, undergoes a peculiar modification and forms the so-called VELAMEN RADICUM (p. 48), a parchment-like sheath surrounding the roots, and often attaining a considerable thickness. The cells of this enveloping sheath are generally provided with spiral or reticulate thickenings, and lose their living contents. They then become filled with either water or air, depending upon the amount of moisture contained in the surrounding atmosphere. These root-envelopes absorb water like blotting-paper ; when the velamen is filled with water, the underlying tissues impart a greenish tint to the root ; but if it contains only air the root appears white. The epidermis of fruits, and particularly of seeds, exhibits a considerable variety of modifications in its mode of thickening, and in the relations the thickening layers bear to one another. The purpose of these modifications in the epidermis becomes at once evident, when it is taken into consideration that, in the case of fruits and seeds, in addition to protecting and enclosing the internal parts, the epidermis has often to provide for their dissemination and permanent lodgment.

The Vascular Bundle System.—The PRIMARY VASCULAR BUNDLES extend in the form of strands throughout the body of the higher plants. In more transparent stems, such as those of *Impatiens parviflora*, the bundles may be clearly distinguished and their course followed. The arrangement of the bundles of leaves is apparent from the venation. In many parallel-veined leaves the bundles are easily isolated. This is often done accidentally, as when, for example, in picking a leaf of Plantain (*Plantago media*) a pull is given at the same time.

Special strands of tissue serving for the transport of substances through the plant are found in the more highly differentiated Thallophyta; examples are afforded by some of the Red and Brown Seaweeds (Rhodophyceae and Phaeophyceae). In the Laminariaceae these conducting tracts contain elements which closely resemble sieve-tubes (108). The thallus of some Liverworts is traversed by a strand which resembles the nerve of a leaf. Bundles sharply limited from the surrounding tissues first appear in the Mosses; they occur commonly in the leaves, less often in the stems. A fairly simple example of this kind of conducting bundle is that of the stem of *Mnium undulatum*, which is represented in tranverse section in Fig. 161.

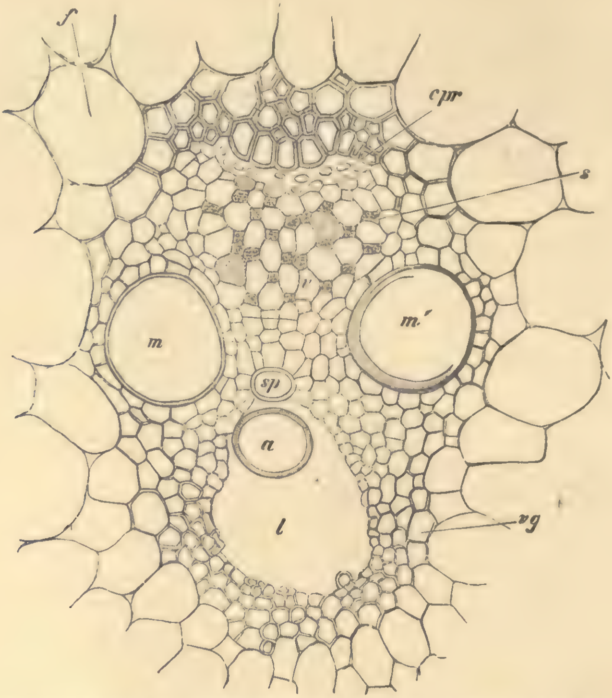


Fig. 121.—Transverse section of a vascular bundle from the internode of a stem of *Zea Mais*. *a*, Ring of an annular tracheid; *sp*, spiral tracheid; *m* and *m′*, vessels with bordered pits; *v*, sieve-tubes; *s*, companion cells; *cpr*, compressed protophloem; *l*, intercellular passage; *vg*, sheath; *f*, cell of fundamental tissue. (× 180.)

Such bundles reach their highest differentiation in the Polytrichaceae. In them the stem has a central cylinder composed of elongated cells with scanty contents, of elements resembling sieve-tubes, and of elongated cells; the three kinds of element serve respectively to transport water, albuminous substances, and carbohydrates (109). The arrangement of the tissue of these complicated strands is often similar to that found in the vascular bundles of more highly organised plants. This is a good example of a striking resemblance between structures which are analogous but have arisen independently in the course of evolution.

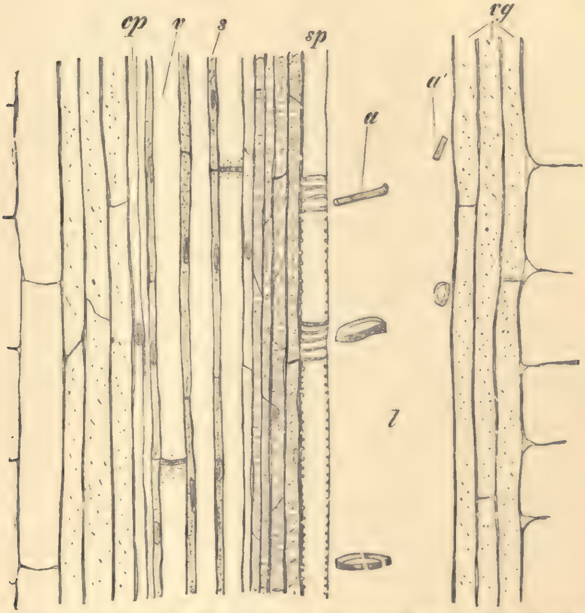


Fig. 122.—Longitudinal section of a vascular bundle from the stem of *Zea Mais.* *a*, and *a′*, Rings of an annular tracheid ; *v*, sieve-tubes ; *s*, companion cells ; *cp*, protophloem ; *l*, intercellular passage ; *vg*, sheath ; *sp*, spiral tracheides. (× 180.)

It is, however, in the Cormophytes, which possess roots, that a high degree of differentiation of the vascular bundles is first attained. Since the absorption of water is limited to the roots, the arrangements in the conducting tracts require to be more perfect. Two distinct components can be distinguished in these vascular bundles, the TRACHEAL or XYLEM PORTION, and the SIEVE-TUBE or PHLOEM PORTION. While these may form independent strands, they are generally united in one VASCULAR BUNDLE. Other terms often used to designate the vascular bundles are FIBRO-VASCULAR BUNDLES and MESTOME. The vascular portion is also termed the XYLEM or

HADROME, and the sieve-tube portion the PHLOEM or LEPTOME (^{110}). The distinction of the two components of the vascular bundle is most evident from transverse sections (Figs. 121, 123), with which the longitudinal section (Fig. 122) should be compared. The vascular portion contains TRACHEÆ and TRACHEIDES as most essential for the fulfilment of its function of water conduction (*a*, *sp*, *m*, Figs. 121, 122), or tracheides alone, and, in addition, living, elongated parenchymatous cells that may be designated XYLEM or WOOD PARENCHYMA. In the phloem portion the most essential elements are the SIEVE-TUBES (*v*), which serve for the conveyance of albuminous matter. They are always accompanied by other living cells; either by the so-called COMPANION CELLS (*s*), or in addition by elongated parenchymatous cells, or by the parenchyma alone. Companion cells only occur in the phloem of Angiosperms. They are sister

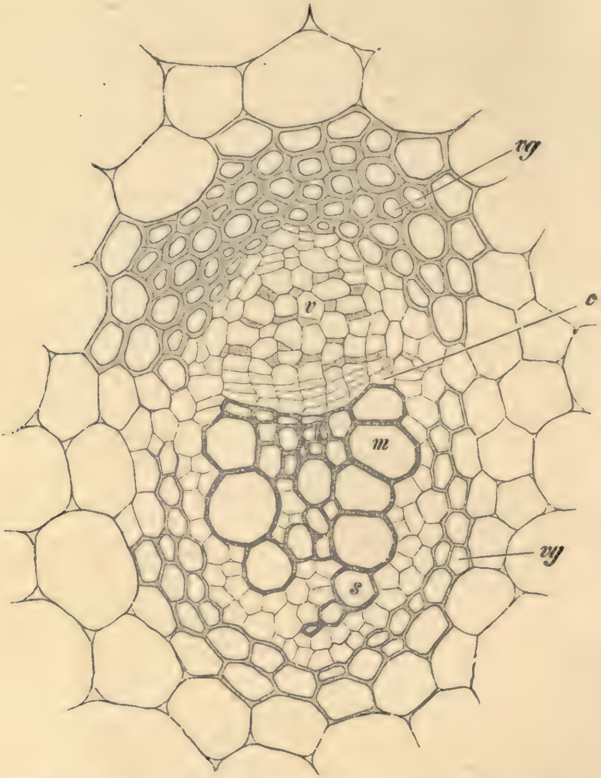


FIG. 123.—Transverse section of a vascular bundle from a stolon of *Ranunculus repens*. *s*, Spiral tracheides; *m*, vessel with bordered pits; *c*, cambium; *v*, sieve-tubes; *vg*, sheath. (× 180.)

cells of the sieve-tubes, having arisen by longitudinal division from the same mother cell. The companion cells are not so large as the sieve-tubes, and may be distinguished from them by their more abundant protoplasmic contents, and especially by the fact that they retain their nuclei, while the nuclei of the sieve-tubes soon disappear. In Monocotyledons (Figs. 121, 122), and in the Ranunculaceae among the Dicotyledons (Fig. 123), the phloem consists solely of sieve-tubes and companion cells; in the other Dicotyledons parenchymatous elements are also present, and these are accordingly distinguished as PHLOEM PARENCHYMA; no companion cells are found in Gymnosperms and Pteridophytes, and in addition to sieve-tubes the phloem contains only phloem parenchyma.

The bundles of the Phanerogams (Gymnosperms and Angiosperms) are generally COLLATERAL in structure, that is, the xylem and phloem are in contact on one side only. In stems the most usual arrangement of the two portions of a collateral bundle is that in which the xylem lies nearest the centre; in leaves the xylem portion lies nearer the upper, and the phloem portion nearer the lower surface. Closely allied to the collateral type is the bicollateral type of bundle. In this the xylem is accompanied by phloem both on the outside and inside. Such bicollateral bundles are characteristic of the Cucurbitaceae (111). The xylem and phloem of roots generally form separate strands (Fig. 124 *s*, *v*), and the xylem strands are differently oriented; while in stems the narrow vessels are nearer the centre and the wider nearer the circumference, in roots this order is exactly reversed.

The "CONCENTRIC" vascular bundles of the Pteridophyta (Fig. 125) contain tracheides (*sp*), and only in exceptional cases tracheæ (*sc*). The latter are as a rule wanting in Pteridophyta, although this group goes by the name of Vascular Cryptogams. The water-conducting elements exhibit scalariform thickenings, only the narrowest having spiral markings (*sp*); they are surrounded by xylem parenchyma (*lp*). Outside this comes a zone of tissue consisting of sieve-tubes (*v*) and phloem parenchyma (*s*).

A number of similar vascular bundles are present in the stem of most Ferns and species of *Selaginella*. In *Lycopodium* they are fused into a single central cylinder. In the stem of Equisetaceae vascular bundles of collateral structure appear.

The vascular bundles are developed from strands of meristematic tissue which are called PROCAMBIUM STRANDS. Within each strand a zone of tissue commences to divide tangentially, and behaving as a primary meristem produces to both the inside and the outside new cells in radial order. If the whole meristematic tissue of a procambium strand is exhausted in this process, the vascular bundles are said to be CLOSED; but if any of the meristematic tissue remains in an undifferentiated condition between the xylem and phloem portions, the bundles are spoken of as OPEN (Fig. 123 *c*). The Pteridophytes have, almost without exception, closed bundles; in Monocotyledons also the bundles are always closed (Fig. 121); Gymnosperms and Dicotyledons (Fig. 123), on the contrary, have open bundles.

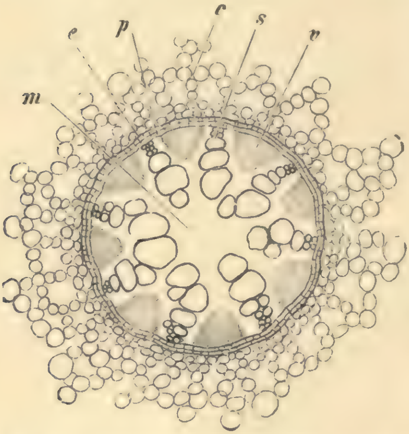


FIG. 124.—Transverse section of central portion of the root of *Acorus Calamus*. *m*, Medulla; *s*, xylem; *v*, phlœm; *p*, pericycle; *e*, endodermis; *c*, cortex. (× 90.)

In those portions of plants which are still actively growing in length, the procambium strands remain undifferentiated, except at definite points, where single rows of cells lose their meristematic condition and form narrow, annular, and spiral vessels and sieve-tubes, or sieve-tubes and companion cells; the structure of all of these is of such a nature as to render their elongation possible. Such primary vascular elements are termed PROTOXYLEM; while the corresponding sieve elements are in like manner designated PROTOPHLOEM. The protoxylem occupies the innermost, the protophloem the outermost side of a procambium strand, from which a collateral bundle is eventually formed. After the growth in length of any part of a plant ceases, the differentiation of the procambium strand into a collateral vascular bundle is continued from the inner and outer sides of the strand toward the centre.

In fully developed vascular bundles the protoxylem and protophloem cease to perform their functions. The protoxylem elements become compressed and ruptured by the tension resulting from the continued vertical growth (*a* and *a′*, Fig. 122), so that in their stead a lysigenic intercellular space is often formed (Figs. 121, 122). The protophloem elements (cf. Figs. 121, 122) at the same time become disorganised, and their sieve-plates closed by a covering of callus.

In accordance with the inverted orientation of the xylem, the protoxylem of roots is found on the outer, not on the inner side of the vascular strands (Fig. 124).

The Terminations of the Vascular Bundles.—In leaves, particularly in the foliage leaves of Angiosperms, the vascular bundles become much branched until finally they are reduced to extremely fine strands. In the leaves of Gymnosperms this branching of the bundles does not usually take place, but instead, a single vascular bundle frequently runs throughout the whole length of the leaf. The vascular bundles of the reticulately-veined leaves of Dicotyledons illustrate the most extreme form of branching.

The minute distribution of the bundles in the leaf-lamina facilitates the regular conduction of water to all parts of the leaf-tissue, and at the same time renders easier the removal of the assimilated products. In the same degree as the ramifications of the vascular bundles are continued, the bundles themselves become attenuated and simpler in structure (Fig. 126). The vessels first disappear, and only spirally and reticulately thickened tracheides remain to provide for the water conduction. The phloem elements undergo a similar reduction. In Angiosperms, in which the sieve-tubes are accompanied by companion cells, the sieve-tubes become narrower, whilst the companion cells retain their original dimensions. Finally, in the cells forming the continuation of the sieve-tubes, the longitudinal division into sieve-tubes and companion cells does not take place, and TRANSITION CELLS are formed (112). With these the phloem terminates, although the vascular portion of the bundles still continues to be represented by short spiral tracheides. The ultimate branches of the bundles either terminate blindly or anastomose with other vascular bundles.

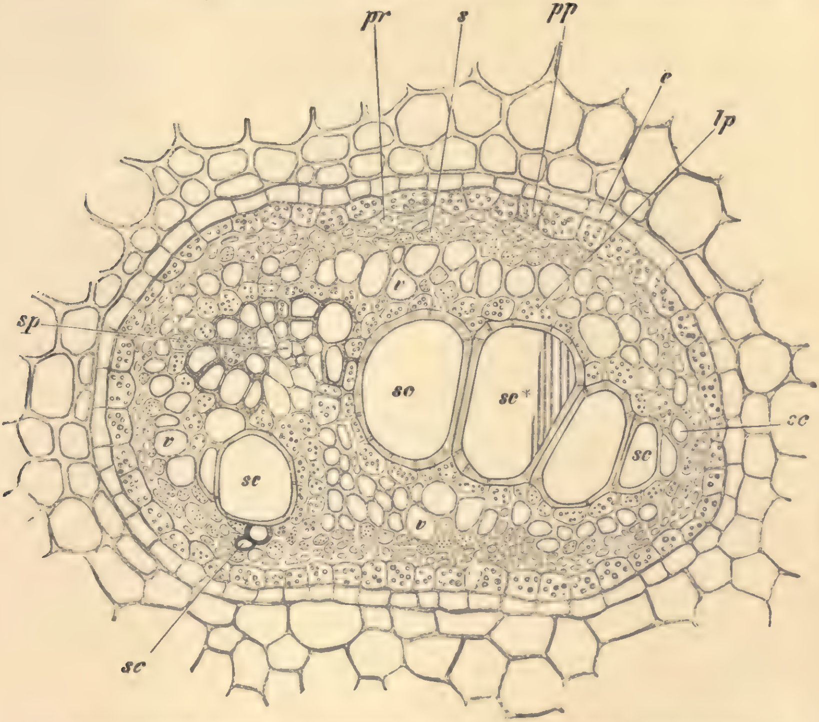


FIG. 125.—Transverse section of a concentric bundle from the petiole of *Pteris aquilina*. *sc*, Scalariform vessels; *sp*, protoxylem (spiral tracheides); *sc**, part of a transverse wall showing scalariform perforations; *lp*, xylem parenchyma; *v*, sieve-tubes; *pr*, protophloem; *pp*, starch layer; *e*, endodermis; *s*, phloem parenchyma. (× 240.)

The Fundamental Tissue System usually forms the main bulk of the primary tissues of the body of a plant. The whole tissue of the lower plants, as it shows no internal differentiation, may, in a certain sense, be considered fundamental tissue. The other tissues have gradually arisen from the fundamental tissue in the course of phylogenetic development. The fundamental tissue in the higher plants is enclosed by tegumentary tissue, and traversed by the vascular bundle system. While the tegumentary tissue protects the plant externally, and the vascular bundle system performs the office of conduction, and also of mechanically strengthening the plant, the duty of providing for the nutrition of the plant and of storing reserve food material falls chiefly to the fundamental tissue. The fundamental tissue consists, therefore, for the most part of parenchymatous cells containing chlorophyll, at least to such depth as the light penetrates; internally a colourless parenchyma is found. The fundamental tissue system also takes part in providing for the mechanical rigidity of plants, and in connection with this function it possesses collenchyma (Fig. 74 *c*) and sclerenchyma as its special mechanical tissues. The COLLENCHYMA (p. 68) is unlignified and very elastic, and thus fitted for stretching; it is the form of mechanical tissue suitable for those parts of plants still undergoing growth in length. The sclerenchymatous fibres, which are often unlignified but have greatly thickened walls, on the other hand, are formed after growth in length has ceased, and sclereides (p. 73) arise even later. The elongated cells of the fundamental tissue also perform a certain share of the work of conduction, and serve for the transport of carbohydrates. Secondary or waste products, resulting from chemical changes, are also deposited in special cells of the fundamental tissue. Consequently idioblasts (p. 73), containing crystals or rows of crystal-containing cells, are often met with in the fundamental tissues, together with cells, tubes, cavities, or canals containing tannin, gum, resin, ethereal oils, latex, or alkaloids. Such waste products are for the most part deposited near the surface of a plant, in order to serve as a defence against destructive animals, or that they may afterwards be thrown off along with the superficial tissue. Cells containing these waste products, particularly crystal cells and latex tubes, are often found, accompanying the phloem portion of the vascular bundles.

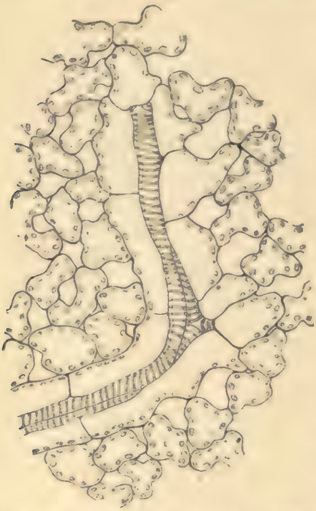


FIG. 126.—Termination of a vascular bundle in a leaf of *Impatiens parviflora*. (× 240.)

The Aroideae, Nymphaeaceae, and several other plant families possess a peculiar form of idioblast, in the so-called internal hairs, which project into the intercellular spaces of the fundamental tissue. In the wide intercellular passages of the petioles and flower stems of the Water-Lily these idioblasts are stellate in form. Their walls are strongly thickened, and provided with short protuberances in which small crystals of calcium oxlate are deposited.

The Distribution of the Primary Tissues (113)

In the body of multicellular plants a distinction between an outer small-celled and firm tissue and an inner large-celled looser tissue soon becomes apparent. The outer tissues are best adapted for protection, the inner for conduction and storage. The cells of the inner tissues accordingly become elongated for the purpose of conduction. The outer tissues in plants, which must provide independently for their own nourishment, contain chromatophores fitted for assimilation, and are correspondingly coloured, while the inner tissues remain colourless. The outer portion of the fundamental tissue thus differentiated is called the CORTEX, the inner the MEDULLA or PITH. An epidermis, distinguishable from the cortex, is found in some of the Mosses, but a sharp distinction between these tissues is first found in the more highly organised plants.

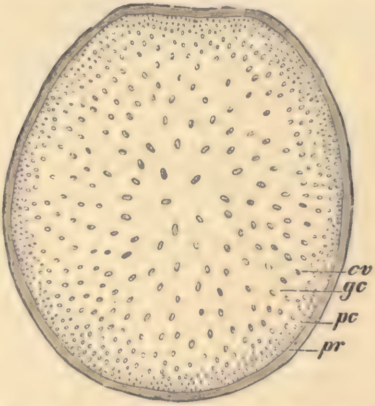


FIG. 127.—Transverse section of an internode of the stem of *Zea Mais*. *pr*, Primary cortex; *pc*, pericycle; *cv* vascular bundles; *gc*, fundamental tissue of the central cylinder. (× 2.)

In the **Stem** of a Phanerogamic plant there is an outer skin or epidermis (Fig. 128 *B*, *e*) on the external surface; then follows the PRIMARY CORTEX (Figs. 127, 128 *A*, *pr*), and internal to this the so-called CENTRAL CYLINDER, for which VAN TIEGHEM has proposed the name STELE (column) (114). The innermost layer of the primary cortex, which may be designated by the term PHLOEOTERMA, is for the most part not distinctly differentiated, but can be recognised in the aerial stems of land-plants as a starch-sheath; while in the rhizomes of land-plants and in the stems of water-plants it forms the ENDODERMIS. Differentiated as a starch-sheath (Fig. 128 *A*, *B*, *st*), the phloeoterma is rendered conspicuous by the quantity of movable starch contained in its cells. A starch-sheath is often present in the young shoots, while it disappears or becomes limited to certain parts of the older shoots (115). When developed as an endodermis, portions of the lateral walls of its cells become suberised (116). In a cross-section these suberised portions of the cell walls of the endodermis appear as dark spots (Fig. 130), but in a tangential section as a wavy band. The CENTRAL CYLINDER of the stem contains vascular bundles (*cv*), which, in the Equisetaceae, the Gymnosperms and Dicotyledons (Fig. 128 *A*), are arranged in a circle, whereas in Monocotyledons (Fig. 127) they are irregularly distributed. In all these cases the xylem portion of the vascular bundle is directed towards the centre, and the phloem portion away from the centre of the stem. That part of the peripheral tissue of the central cylinder lying outside of the bundles is called the PERICYCLE (*pc*). If the bundles are arranged in a circle (Fig. 128 *A*), that part of the central cylinder enclosed by them is the PITH or MEDULLA (*m*), and the tissue between the different bundles the PRIMARY MEDULLARY RAYS. In the case of scattered bundles (Fig. 127), a distinction between medulla and medullary rays is no longer possible. Wherever there is no sharp distinction between primary cortex and central cylinder, comparative investigation alone can determine whether a tissue belongs to the primary cortex or to the central cylinder.

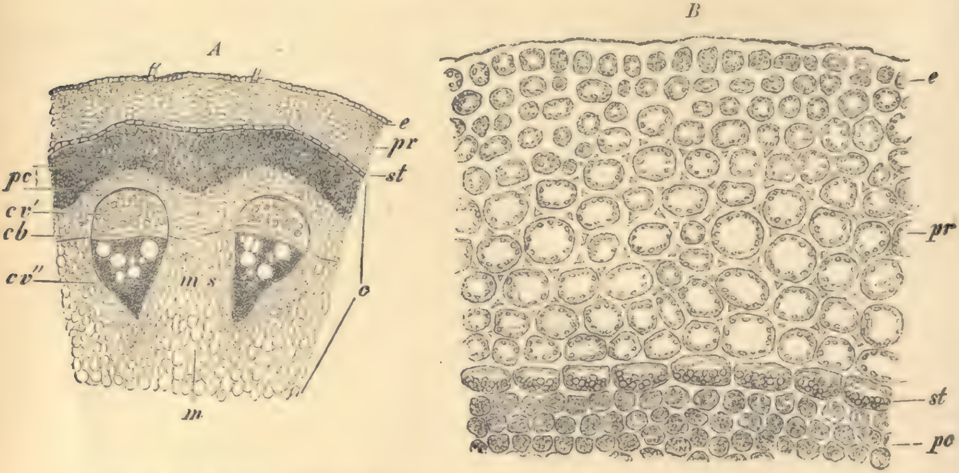


FIG. 128.—*A*, Part of a transverse section of a young stem of *Aristolochia Sipho*. *e*, Epidermis; *pr*, primary cortex; *st*, starch-sheath; *c*, central cylinder; *pc*, pericycle, in this case with a ring of sclerenchyma fibres; *cv'*, phloem, and *cv''*, xylem portions of the vascular bundle; *cb*, cambium ring; *m*, medulla; *ms*, primary medullary ray. (× 48.) *B*, Small portion of the periphery of a similar section of a still younger stem. *e*, Epidermis; *pr*, primary cortex; *st*, starch-sheath with easily movable starch grains; *pc*, outer layers of the pericycle. (× 350.)

Although the fundamental tissue of the primary cortex is mainly a chlorophyll-containing tissue, portions bordering on the epidermis frequently become converted, for mechanical purposes, into strands of collenchyma or sclerenchyma. Such a mechanical tissue, which serves to strengthen the epidermis, is known as a HYPODERMA. Of the tissues composing the central cylinder, the pericycle, the primary medullary rays, and medulla consist of fundamental tissue, and are chiefly composed of colourless parenchyma. A part, however, of the tissue of the pericycle may become sclerenchymatous (Fig. 128 *A*, *pc*); sclerenchymatous elements also often surround individual bundles as sheaths, or accompany the phloem portion in the form of strands (Figs. 121, 123). Whenever such a sheath of sclerenchyma is developed about a bundle, it is interrupted on both sides of the bundle, at the junction of the xylem and phloem portions, by parenchymatous cells, or by cells which are only slightly thickened and lignified. The existence of these unthickened places facilitates the exchange of water and food material between the vascular bundles and the fundamental tissue. When a common starch-sheath is not present in a stem, starch-sheaths are sometimes

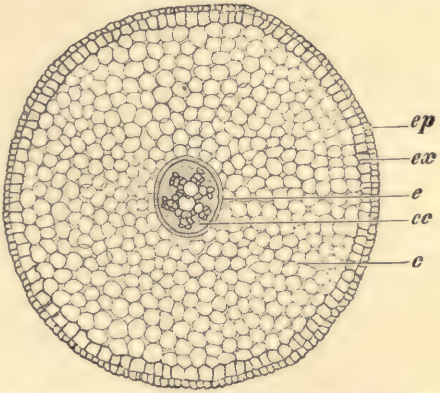
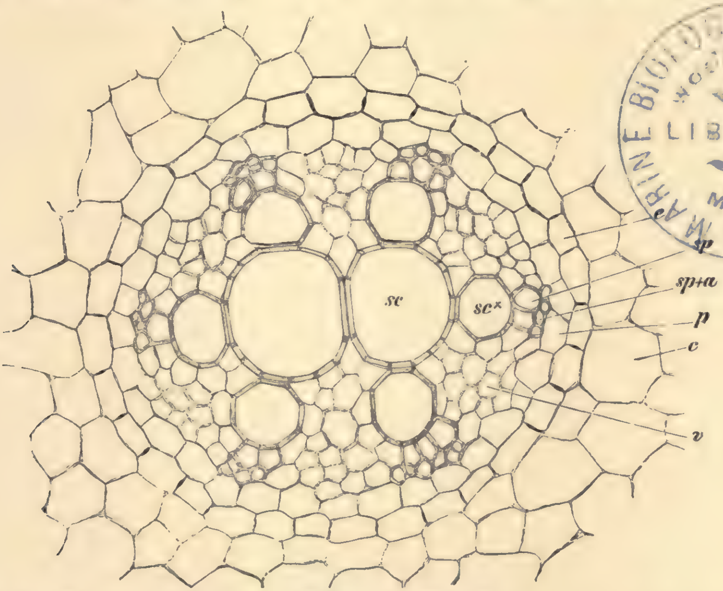


FIG. 129.—Transverse section of an adventitious root of *Allium Cepa*. *ep*, Remains of the epidermis; *ex*, exodermis; *c*, primary cortex; *e*, endodermis; *cc*, central cylinder. (× 45.)



MARINE BIOLOGICAL LABORATORY LIBRARY WOODS HOLE, MASS.

FIG. 130.—Transverse section of an adventitious root of *Allium Cepa*. *c*, Primary cortex; *e*, endodermis; *p*, pericycle; *a*, annular tracheides; *sp*, spiral tracheides; *sc* and *sc**; scalariform vessels; *v*, phloem. (× 240.)

found surrounding the individual vascular bundles, or particular rows of cells provided with movable starch grains are present. The central cylinder of Phanerogams is simple, and occupies a more or less central position. In a few cases, as in the stems of *Auricula* and *Gunnera*, the central cylinder is broken up into several partial cylinders.

In **Roots**, the division between primary cortex and central cylinder is sharply marked by the endodermis, into which the innermost layer of the primary cortex is usually transformed (Figs. 124, 129, 130 *e*). The central cylinder becomes completely shut off from the primary cortex by the suberisation of the lateral walls of the endodermal cells, and by their close and uninterrupted contact. While, by this means, the passage of gases from the intercellular spaces of the cortex into the central cylinder, with the consequent obstruction of the water-channels, is prevented, the passage of water from the cortex to the central cylinder can, at the same time, go on unhindered through the unsuberised inner and outer walls of the endodermal cells. In this manner it is possible for the water, absorbed from the soil by the root-hairs or by the surface of the roots, to be transferred to the tissues of the central cylinder. In the older parts of the roots, which no longer absorb water from the soil, the cells of the endodermis become greatly thickened, but generally on one side only; they may also be cutinised. Should thickening occur at an early stage, special endodermal cells, directly external to the xylem strands, remain unthickened and serve as TRANSFUSION CELLS (Fig. 131 *f*).

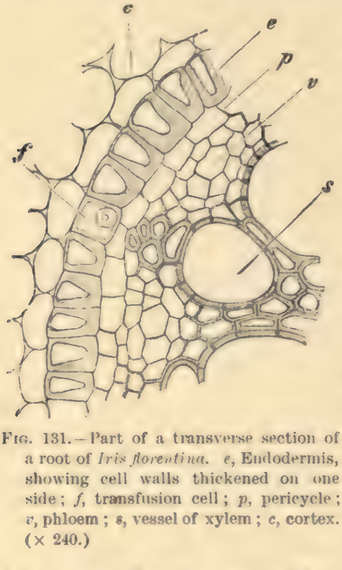


FIG. 131.—Part of a transverse section of a root of *Iris florentina*. *e*, Endodermis, showing cell walls thickened on one side; *f*, transfusion cell; *p*, pericycle; *v*, phloem; *s*, vessel of xylem; *c*, cortex. (× 240.)

While the root-hairs are as a rule developed from the cells of a definite region of the epidermis, they may, in case the epidermis is thrown off at an early stage, arise from the outermost cortical layer, which then assumes the functions of an epidermis. In any case the epidermis soon disappears, and the outermost cortical layer becomes cuticularised and, as an EXODERMIS, takes its place. Frequently some of the cells of such an exodermis remain uncutinised and serve as transfusion cells. They may be characterised by their smaller size, and be regularly distributed between the cutinised cells. In aerial roots the epidermis usually forms a many-layered root-sheath or velamen (cf. p. 109), within which comes the exodermis.

The primary cortex of the root is composed of colourless tissue, which is usually parenchymatous. In the outer layers the cells are in close contact with one another, but intercellular spaces are present more internally. These intercellular spaces often widen into air-cavities or passages. In many roots a hypoderma giving mechanical support to the epidermis or exodermis is present. The outermost layer of cells of the central cylinder (Figs. 124, 131 *p*) forms the pericycle, which is also called the pericambium ; this is usually a single layer, and in rare cases is wanting. The xylem and phloem portions form separate strands (p. 113), radially disposed and alternating with each other (Figs. 124, 130). It has already been shown that the narrowest elements of the vascular strand are outermost. Roots are described as diarch, triarch, polyarch, according to the number of the vascular strands. For example, the roots of *Acorus Calamus* (Fig. 124) are octarch, those of *Allium Cepa* (Fig. 130) hexarch. The vascular strands may either meet in the centre (Fig. 130), or they may surround a central pith (Fig. 124).

The **Leaves** are composed of fundamental tissue (which is here termed mesophyll), bounded by an epidermis and traversed by vascular bundles. Sheaths are present around the bundles, extending to their fine terminations. The cells composing these mesophyll sheaths are as a rule elongated and not separated by intercellular spaces. Besides limiting the vascular bundles from the mesophyll, the sheaths perform the important function of conducting soluble carbohydrates from the leaf to the stem. The larger vascular bundles are usually accompanied by strands of sclerenchyma ; these disappear from the finer branches. Other strands of sclerenchyma not connected with the vascular bundles may also occur in the mesophyll and contribute to the rigidity of the leaf.

The mesophyll passes into the primary cortex of the stem, while the vascular bundles are continuous with the central cylinder. Thus in the leaf, tissues corresponding to the cortex and central cylinder of the stem remain distinct from one another.

The mesophyll of the coloured FLORAL LEAVES of the Angiosperms usually consists of a somewhat loose tissue, containing intercellular spaces and traversed by vascular bundles. The laminæ of many assimilating FOLIAGE LEAVES, especially of shade-loving plants, may have a similar uniform structure; but they are usually more complicated, and exhibit a difference in the structure of their upper and lower sides (Fig. 132). In such dorsiventral structures the upper epidermis is succeeded by one or more layers of cylindrical parenchymatous elements elongated at right angles to the surface, and known as the PALISADE CELLS. These are especially rich in chlorophyll, and are often separated laterally from one another, so that the conduction of substances is limited to the direction of their longer axis (Fig. 132). Adjoining the palisade parenchyma, and extending to the epidermis (*ep''*) on the under surface of the leaf, is a loose tissue called the SPONGY PARENCHYMA. In contrast to the palisade cells, the cells of the spongy parenchyma are less abundantly supplied with chlorophyll; they are also much more irregular in shape, and have large intercellular air-spaces between them. The palisade cells are elongated in the direction in which the rays of light penetrate the leaf-lamina, and by this means are particularly adapted to their special function of assimilation. The spongy parenchyma, on the other hand, is arranged to facilitate the free passage of gases, and to that end develops large intercellular spaces in direct communication with the stomata of the lower epidermis. HABERLANDT (117) has estimated that to every square millimetre of surface in a leaf of *Ricinus communis* there are, in the palisade cells, 403,200 chlorophyll granules; in the cells of the spongy parenchyma only 92,000; that is, 82 per cent of all the chlorophyll granules belong to the upper surface of the leaf, and only 18 per cent to the under side. The palisade cells are often arranged in groups, in which the lower ends of the cells of each group converge (Fig. 132). In this way several palisade cells come into direct contact with a single expanded cell of the spongy parenchyma, which thus functions, apparently, as a collecting cell for a group of palisade cells. The products of assimilation are passed on from the collecting cell through the spongy parenchyma, to be finally carried to the mesophyll sheath surrounding the vascular bundles. The sheaths serve as a conducting tissue towards the stem.

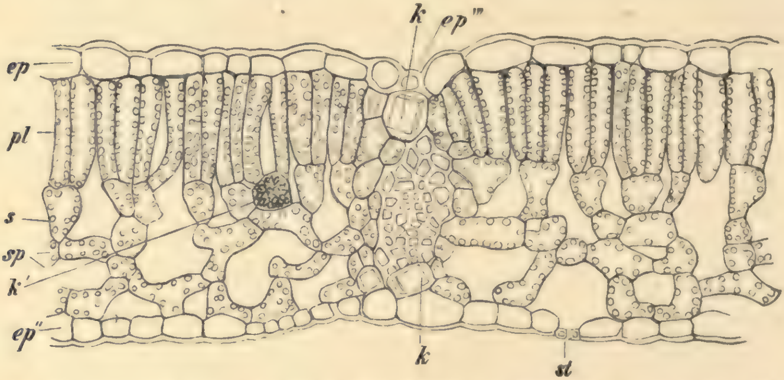


FIG. 132.—Transverse section of a leaf of *Fagus sylvatica*. *ep*, Epidermis of upper surface; *ep''*, epidermis of under surface; *ep'''*, elongated epidermal cell above a vascular bundle; *pl*, palisade parenchyma; *s*, collecting cells; *sp*, spongy parenchyma; *k*, idioblasts with crystals, in *k'* with crystal aggregate; *st*, stoma. (× 360.)

At the base of the lamina the tissues close together and pass into the leaf-stalk, where one is present. The dorsiventral structure becomes less marked in the petiole. The cells are mostly elongated in the length of the petiole, a modification which facilitates the conduction of food material. They are often thickened and so arranged as to meet the altered requirements for mechanical rigidity. The vascular bundles pass from the leaf-stalk into the stem and there either arrange themselves among the bundles of the central cylinder or at once fuse with some of them. In the leaf-stalks of Angiosperms the bundles usually appear arranged in a curve open above, but may form other figures. In the petioles of Ferns, the partial cylinders are accompanied, as in the stem, by sclerenchymatous fibres forming strands or plates. It is the peculiar arrangement of those brown-walled sclerenchymatous masses which forms the double eagle apparent on cross-sections of the petiole of *Pteris aquilina*, from which the plant derives its specific name.

In certain families of the Dicotyledons, particularly in the Crassulaceae, the mesophyll of the leaf-lamina forms peculiar masses of tissue called the EPITHEMA between the swollen terminations of the bundles and the epidermis. The cells of the epithema are small and, for the most part, devoid of chlorophyll ; they are full of water, and joined closely together, leaving only very small interspaces, which are filled with water. They are internal hydathodes (cf. p. 108) and serve for the active excretion of water. Water pores are usually situated above such epithemata. The leaf-tips of a number of aquatic Monocotyledons show a depression into which the terminations of tracheides project. These depressions arise by the destruction of water-pores or of these together with the epidermis. They may be closed by the persisting cuticle. These apical openings serve in the same way for the excretion of water (118).

The Course of the Vascular Bundles (119).—The bundles exhibit a definite course and arrangement within the body of a plant. It is sometimes possible, by maceration, to obtain preparations in which the course taken by the bundles may be followed. By allowing a leaf, stem, or flower to lie in water until it has become softened and disintegrated, a skeleton formed by the more imperishable vascular system may be obtained.

Vascular bundles which pass from a leaf into a stem form within the latter what are known as LEAF-TRACES. The leaf-traces may be composed of one or more vascular bundles, and are accordingly distinguished as one-strand or many-strand leaf-traces. When, as is usually the case, the vascular system of the stem is entirely composed of leaf-traces, each vascular bundle of the trace after passing downwards for some distance unites with another entering from a lower leaf. The arrangement of the bundles in a stem varies according to the distance and direction traversed before the coalescence of the bundles takes place. A relatively simple case is afforded by the young twigs of the Dwarf Juniper (*Juniperus nana*) (Fig. 133). The leaves are in whorls of three, the leaves of successive whorls alternating with one another. From each leaf a leaf-trace consisting of a single vascular bundle enters the stem. This divides into two about the middle of the internode below, and the divisions diverge and unite with the leaf-traces of the whorl below. The arrangement of the bundles may be shown diagrammatically by representing the bundles as if on the surface of an unrolled cylinder, so that they all appear in one plane. This is done in Fig. 133, which also shows the origin of the vascular bundles of the axillary shoots (k).

The arrangement of the bundles in the Yew (*Taxus baccata*), although its leaf-traces have only one bundle, is much more complicated (Fig. 134), for the bundles maintain a distinct course throughout twelve internodes before coalescing. Each bundle at first descends in a straight direction through four internodes; it then curves to the side to give place to a newly-entering leaf-trace, with which it finally coalesces at the twelfth internode. The position of a leaf necessarily determines the point of entrance of its leaf-trace into the stem, and accordingly a diagram (Fig. 134) of the bundles of *Taxus* will exhibit a divergence of the leaf-traces corresponding to the $\frac{5}{13}$ divergence of the leaves. The course taken by the leaf-traces in the stem, however, is independent of the leaf position, and varies considerably in different stems, although the divergence of their leaves may be the same. The stem of *Clematis viticella* affords an example of leaf traces consisting of three vascular bundles. The leaves are in whorls of two, the successive whorls alternating with one another. The median strand of each leaf-trace (Fig. 135 *ad*, *ak*, *nq*, *tx*) has a free course through one internode, and at the node below divides into two arms which coalesce with the adjacent lateral strands of the leaves inserted at this node. The two lateral strands of each leaf-trace (Fig. 135 *bc*, *ef*, *hi*, *lm*, *op*, *rs*) also are free throughout the internode, but at the node below curve inwards and become attached to the same lateral strands as the arms of the median bundle of the trace.

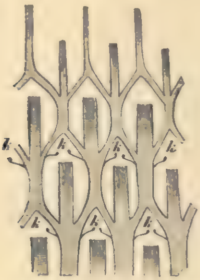


FIG. 133.—Diagram of the course of the vascular bundles in a young branch of *Juniperus nana* shown on the unrolled surface of the cylinder. At *kk* the vascular bundles passing to the axillary shoots are seen. (After GEYLER.)

The traces of the axillary buds of most Gymnosperms and Dicotyledons unite to form two strands which enter the mother shoot and are inserted upon its leaf-traces (Fig. 133 k).

As a general rule, the leaf-trace bundles in Gymnosperms and Dicotyledons arrange themselves in a circle in the stem. There are, however, Dicotyledons in which the vascular bundles form two (*Cucurbita, Phytolacca, Piper*) or more circles (*Amarantus, Papaver, Thalictrum*). In such cases the inner circle is usually more or less irregular.

In the stems of Monocotyledons (Fig. 127) the vascular bundles are scattered, and without any apparent regular order. Their scattered arrangement is due to the varying distances to which the bundles of the leaf-traces penetrate into the central cylinder of the stem. This results from the prolonged growth in thickness of the growing point after the procambial strands have been laid down (120). A common arrangement of the bundles in monocotyledonous stems is that of the so-called Palm type, in which each leaf-trace consists of

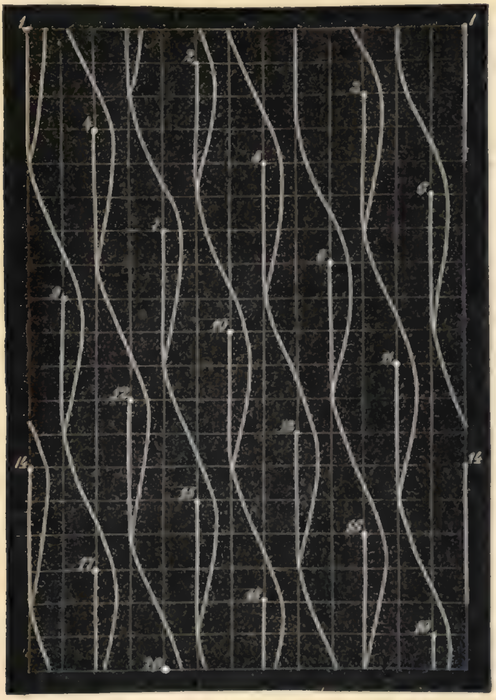


FIG. 134.—Diagram showing the course of the vascular bundles in a shoot of *Taxus baccata*.

the numerous bundles which pass singly into the stem from the broad leaf-base. The median bundle penetrates to the middle of the stem. The depth to which the lateral bundles penetrate varies with their remoteness from the median bundle. In their descending course the bundles gradually curve outwards, and finally join other bundles near the periphery of the stem. The number of internodes, therefore, through which a bundle passes before coalescence, is variable; the median bundle, however, continues distinct for the longest distance. The deeper penetration and greater length of the median bundle become apparent in a median longitudinal section of such a stem

(Fig. 136). The numerous bundles entering the stem from axillary shoots pursue a similarly curved course to those entering from leaves.

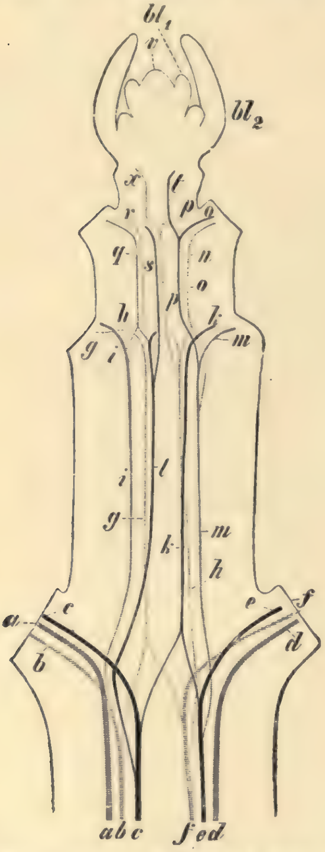


Fig. 135.—*Clematis viticella.* End of a branch which has been made transparent by the removal of the superficial tissues and treatment with caustic potash. The emerging strands have been slightly displaced by gentle pressure. The two uppermost pairs of young leaves (bl^1, bl^2) are still without leaf-traces. *v*, Apical cone. (After Nägeli.)

In addition to the leaf-trace bundles or COMMON BUNDLES, which are common to both leaf and stem, there are others, called CAULINE BUNDLES, which belong solely to the stem, and again others, FOLIAR BUNDLES, which, on entering the stem from the leaf, at once coalesce with other bundles and have no independent existence in the stem. The bundles of the Pteridophytes are continued as cauline bundles in the stem, and those from the leaves join on to the bundles of the stem.

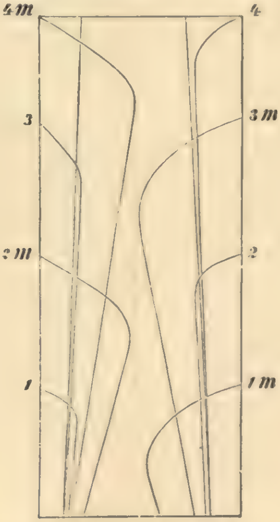


Fig. 136.—Diagram showing the course of the vascular bundles of Monocotyledons of the Palm type, with alternating, two-ranked amplexicaul leaves. The numbers indicate the sequence of the leaves; *m*, median bundle. (After De Bary.)

The stems of many Dicotyledons (*Begonia, Aralia*) possess cauline bundles in addition to leaf-traces. The cauline bundles are situated in the pith within the ring of leaf-trace bundles in the internode, and at the nodes are connected by branches with the leaf-trace bundles.

In the central cylinder of roots, the radially arranged strands of xylem and phloem pursue a straight course parallel to one another. The xylem and phloem strands of lateral roots are inserted upon the corresponding strands of the parent root. Those of adventitious roots are attached to the corresponding tissues of the stem or root from which the adventitious root arises. The strands of xylem and phloem of the main root of a phanerogamic seedling are continuous with the leaf-trace bundles in the hypocotyl (120).

Increase in Thickness by Continued Enlargement of the Primary Meristem.—The growing points of those Monocotyledons which have large stems (Palms, Pandanaceae, some Liliiflorae) exhibit this feature. The growing point thus attains a considerable thickness, and the stem has from an early period its definite circumference. The increase in number of cells takes place in a zone lying at the periphery of the growing point (121).

A Special Form of Growth in Thickness of the Stem by means of the Continued Enlargement of the Fundamental Tissue.—This is often exhibited by Palms, and leads in them to the formation of stems which may be more than 1 metre in diameter. EICHLER (122) has shown that the growth in thickness is solely due to the continued expansion of the already existing cells of the fundamental tissue of the central cylinder. In this process, by the expansion of the cell lumen and increased thickening of the walls, the strands of sclerenchymatous fibres accompanying the vascular bundles on their phloem sides also become greatly enlarged. In this form of growth in thickness no new elements are formed.

Enlargement due to Continued Cell Divisions in the Fundamental Tissue.—This is seen most strikingly in the growth of the fruits of many Angiosperms. In their development from the small rudiment in the flower there may be a great increase in size, although no new meristematic tissue has been formed. The growth is due to repeated divisions in the epidermal cells and in those of the fundamental tissue. The tissue thus produced may when mature be thin-walled, or its cells may undergo various changes in form and in the thickness of their walls. From small structures such large fruits as those of the Gourds may develop in this way.

The Secondary Tissues (123)

After growth in length is finished through the activity of a cambial tissue, functioning either as a primary or secondary meristem (p. 99), secondary tissues are added to the previously existing primary tissues, or even substituted for them. Although, phylogenetically considered, secondary tissues seem to have been developed first in the Pteridophytes in forms now only known in a fossil condition (Calamarieae, Sigillarieae, Lepidodendreae) they first became of general occurrence in the Phanerogams. In them the formation of secondary tissues is almost exclusively confined to the roots and stems; secondary growth is met with in some foliar structures but only in a slight form.

Cambium (124).—The primary and secondary meristems, the activity of which gives rise to secondary growth, are given the name of CAMBIUM. These tissues persist in a meristematic condition and undergo successive divisions by walls parallel to one another, so that the cells produced from them are arranged in radial rows. A similar mode of division characterises the primary meristem in the procambial strands, which give rise to collateral vascular bundles (cf. p. 113), and this might also come under the term cambium. It is advisable, however, to restrict this term to meristems giving rise to secondary growth. As a rule the cambium forms new tissue-elements on both sides, but cases are not wanting in which this takes place to one side only.

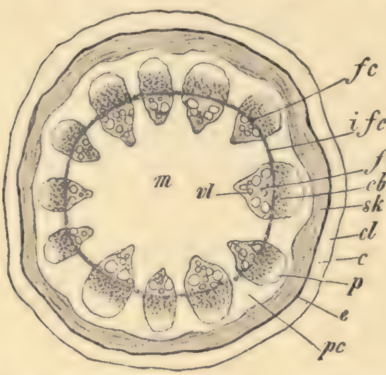


FIG. 137.—Transverse section of a stem of *Aristolochia Sipho* 5 mm. in thickness. *m*, medulla; *fv*, vascular bundle; *vl*, xylem; *cb*, phloem; *fc*, fascicular cambium; *ifc*, interfascicular cambium; *p*, phloem parenchyma; *pc*, pericycle; *sk*, ring of sclerenchyma; *e*, starch-sheath; *c*, primary cortex; *cl*, collenchyma in primary cortex. (× 9.)

As a rule a single persisting initial layer is present in the cambium from which on one or both sides the rows of cells take their origin. In many cases in which the cambial activity is confined to one side, according to J. C. SCHOUTE, the original initial cells are used up in the tissue formation, and new initial cells arise from adjoining cells of the ground-tissue.

Growth in Thickness of the Stem in Gymnosperms and Dicotyledons.—The cambium of the open vascular bundles of Gymnosperms and Dicotyledons, which exhibit a growth in thickness, commences its activity almost directly after the formation of the primary tissue. The primary meristem remaining between the xylem and phloem of the bundle continues its active growth as the cambium. Its cells are full of protoplasm and continue to divide by means of tangential and occasionally radial walls. The new cells thus continuously given off from the initial cells toward the xylem and phloem sides of the bundles experience another tangential division before attaining their definite form as elements of the xylem or phloem portions. The vascular bundles of Gymnosperms and Dicotyledons which undergo secondary growth are usually arranged in a circle. After the cambium in the bundles begins its activity, a zone of tangentially dividing tissue, called the INTERFASCICULAR CAMBIUM, develops in the primary medullary rays between the original bundles, and, uniting with the cambium in the bundles, forms a complete cambium ring. This cambium ring is thus composed of two distinct forms of meristematic tissue; for while the cambium of the bundles or the FASCICULAR CAMBIUM consists of primary meristem (p. 99), the connecting zone of interfascicular cambium is of later development, and is consequently a secondary meristem (p. 99). A cross-section of a young stem of *Aristolochia Sipho*, with the cambium ring in process of formation, is represented in Fig. 137; in Fig. 138 a single bundle of the same cross-section, more highly magnified, shows the fascicular cambium with the interfascicular cambium to either side in a condition of

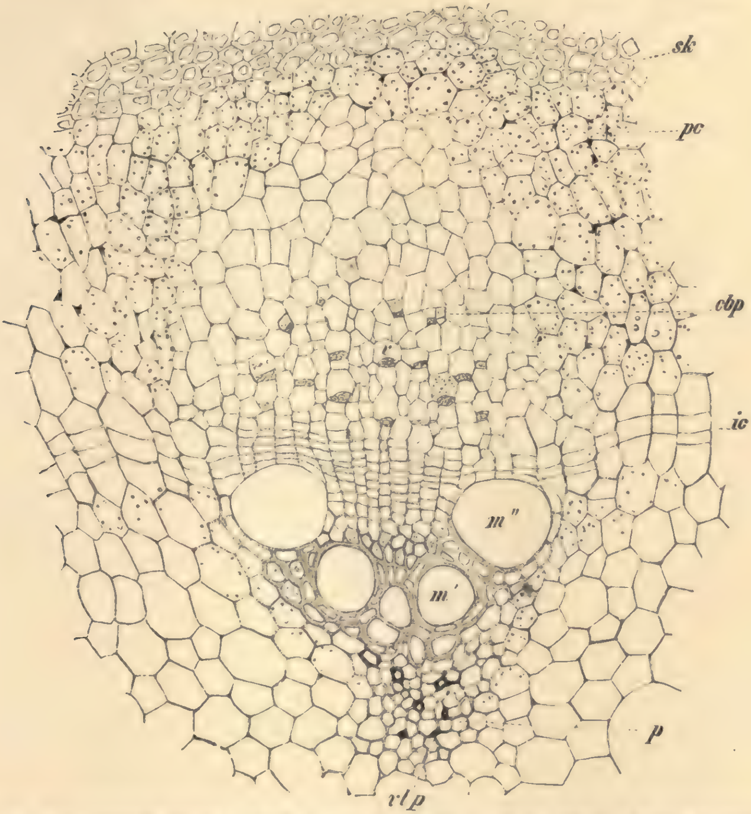


FIG. 138.—Transverse section of a stem of *Aristolochia Sipho* in the first year of its growth, showing a vascular bundle with cambium in active division. *p*, Vascular parenchyma; *vlp*, protoxylem; *m'* and *m''*, vessels with bordered pits; *ic*, interfascicular cambium in continuation with the fascicular cambium; *v*, sieve-tubes; *cbp*, protophloem; *pc*, pericycle; *sk*, inner part of ring of sclerenchymatous fibres. (× 130.)

active division. Within the bundle may be seen two large vessels (m''), in a still incomplete state; while in the adjoining primary medullary rays the cells which give rise to the interfascicular cambium may still be plainly distinguished. All the tissue arising from the inner side of the cambium ring goes to form the secondary WOOD, while that produced on the outside is termed secondary BAST. The vascular portions of the wood form the WOOD STRANDS, the sieve portions within the bast the BAST STRANDS. By the activity of the interfascicular cambium, the primary medullary rays are continued throughout both the wood and bast. As the wood and bast strands enlarge, SECONDARY MEDULLARY RAYS are developed from the fascicular cambium. In one direction the secondary medullary rays terminate blindly in the wood, and in the other in the bast; the later they develop, the less deeply they penetrate the tissues on either side of the cambium.

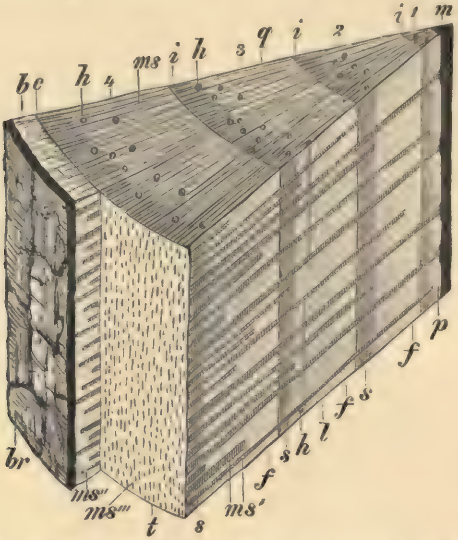


FIG. 139.—Portion of a four-year-old stem of the Pine, *Pinus sylvestris*, cut in winter. *q*, Transverse view; *l*, radial view; *t*, tangential view; *f*, spring wood; *s*, autumn wood; *m*, medulla; *p*, protoxylem; 1, 2, 3, 4, the four successive annual rings of the wood; *i*, junction of the wood of successive years; *ms*, *ms'*, *ms'''*, medullary rays in transverse, radial, and tangential view; *ms''*, radial view of medullary rays in the bast; *c*, cambium ring; *b*, bast; *h*, resin canals; *br*, bark external to the first periderm layer, and formed from the primary cortex. (× 6.)

The primary medullary rays are therefore often distinguished as long, the secondary as short medullary rays. The expression transverse parenchyma is also sometimes used to designate the medullary rays, which are in fact composed almost exclusively of parenchymatous tissue. The cells given off by the initial layer of the cambium for the formation of medullary rays do not undergo a further tangential division, as in other cases, but assume at once the character of medullary ray cells.

The cambium cells have, for the most part, the shape of right-angled prisms, of which the radial diameter is smaller than the tangential. The ends of these prisms are usually one-sided, tapering to a point, alternately on the right and left sides. The length of the cambium cells varies in different plants, but those from which medullary rays are formed are the shorter. The primary vascular portions of the bundles projecting into the medulla constitute what is known as the MEDULLARY SHEATH.

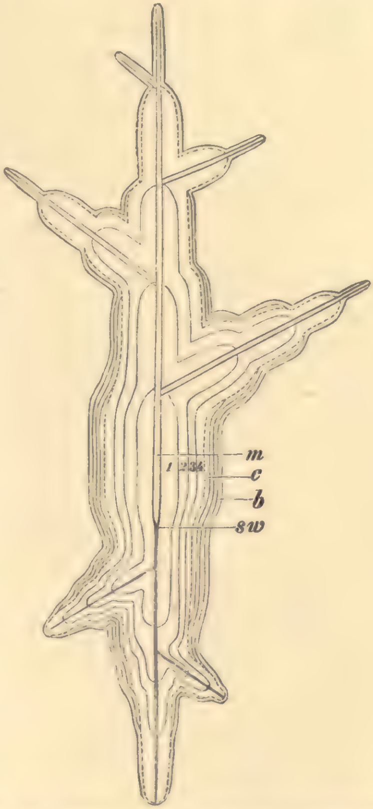


FIG. 140.—Diagram to illustrate the secondary growth in thickness of the stem and root of a Gymnosperm or Dicotyledon. *c*, Cambium, indicated by a dotted line; *m*, pith; 1, 2, 3, 4, successive annual rings of wood; *b*, bast; *sw*, limit between main stem and tap-root.

Owing to climatic variations, the cambial tissue of woody plants exhibits a periodical activity which is expressed by the formation of ANNUAL RINGS of growth (Figs. 139, 141 *A*, 146). In spring, when new shoots are being formed, wider tracheal elements are developed than in the following seasons (Figs. 141 *A*, 148). For this reason a difference is perceptible between the EARLY WOOD (spring wood), which is composed of large elements especially active in the conveyance of water (Fig. 141 *f*), and the LATE WOOD (autumn wood), consisting of narrow elements which impart to a stem its necessary rigidity (Fig. 141 *s*). Throughout the greater part of the temperate zone, the formation of wood ceases in the latter part of August until the following spring, when the larger elements of the spring wood are again developed. Owing to the contrast in the structure of the spring and the autumn wood, the limits (Fig. 139 *i*) between successive annual rings of growth become so sharply defined as to be visible even to the naked eye, and so serve as a means of computing the age of a plant.

Under certain conditions the number of annual rings may exceed the number of years of growth, as, for instance, when MIDSUMMER GROWTH occurs, such as commonly happens in the Oak, when, after the destruction of leaves by caterpillars, a second formation of spring wood is occasioned by the new outgrowths thus induced. In the wood of tropical plants the annual rings may be entirely absent. This occurs, for example, in the tropical Conifers of the genus *Araucaria*, which, in this respect, show a marked contrast to the Conifers of the northern zone. Any interruption of growth, such as would occur during a drought, followed by a period of renewed activity, may occasion the formation of annual rings even in tropical plants.

Although a cessation in the formation of wood takes place so early, the cambium tissue continues to form bast so long as climatic conditions permit. As a rule, however, far fewer elements are added to the bast than to the wood. Owing to the continued growth in length, the higher a cross-section is made of a gymnospermous or dicotyledonous stem the fewer will be the annual rings. As the diagram in Fig. 140 shows, the older rings disappear first on passing towards the apex, and in the same way the older layers of the bast are unrepresented nearer the apex. Up to a certain period, in the age of woody plants, the elements of both wood and bast exhibit a progressive increase in size.

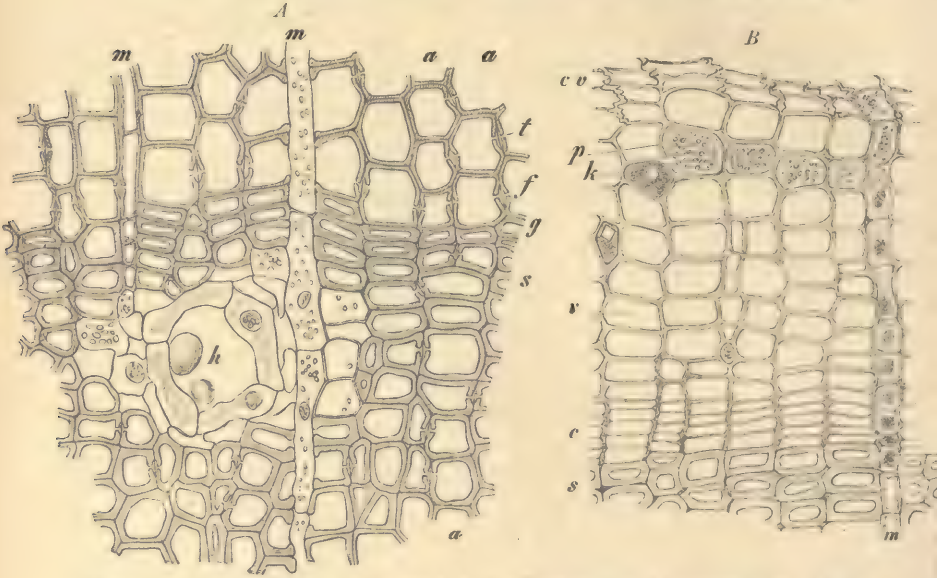


FIG. 141.—*A*, Transverse section of the wood of a Pine at the junction of two annual rings. *f*, Early wood ; *s*, late wood ; *t*, bordered pit ; *a*, interposition of a new row of tracheides resulting from the radial division of a cambium cell ; *h*, resin canals ; *m*, medullary rays ; *g*, limit of late wood. (× 240.) *B*, Part of a transverse section of the stem of a Pine. *s*, Late wood ; *c*, cambium ; *v*, sieve-tubes ; *p*, bast parenchyma ; *k*, cell of bast parenchyma containing crystal ; *cv*, sieve-tubes, compressed and functionless ; *m*, medullary ray. (× 240.)

The living elements may remain in a state of greater or less activity throughout the whole of the wood, extending even to the pith; such wood is called splint wood: the Beech (*Fagus sylvatica*) may be quoted as an example. In other trees which form heart-wood, the living elements die after a certain time, so that only dead tissues are found at a certain distance from the cambium. Before the death of the living cells, they usually produce certain substances, such as tannin and gums, which permeate the cell walls of the surrounding elements, and also partially close their cavities. The tannins impart to the dead wood a distinct colour, often very characteristic, especially when it has been transformed into wood dyes, or so-called XYLOCHROME. The tannin in the woody walls acts as a preservative against decay, while the gums close the functionless water-courses of the dead wood. The dead portion of the wood of a stem is called the HEART-WOOD or DURAMEN, in contrast to the living SAP-WOOD or ALBURNUM. Usually the splint or sap wood is at once distinguishable from the heart-wood by its lighter colour. In some stems, however, the heart-wood does not change its colour. In that case, as the protecting materials are generally absent, it is liable to decay, and then, as so often occurs in the Willow, the stem becomes hollow.

The sap-wood is limited, according to the kind of wood, to a larger or smaller number of the younger annual rings, and to it falls the task of water conduction.

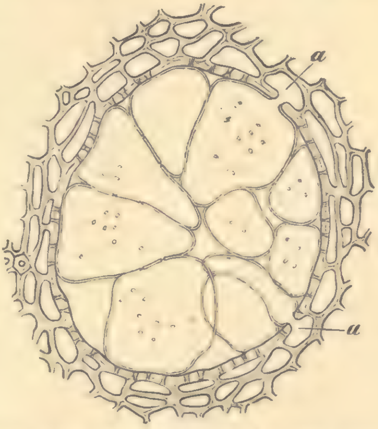


FIG. 142.—Transverse section of a vessel from the heart-wood of *Robinia Pseudacacia*, closed by tyloses; at *a*, *a* is shown the connection between the tyloses and the cells from which they have been formed. (× 300.)

The distinction between sap- and heart-wood is sharpest where the latter is dark-coloured, as in the Oak, with its brown heart-wood, and in species of *Diospyros*, whose black heart-wood furnishes ebony. The darker the heart-wood, the harder and more durable it usually is. The following may be mentioned as examples of woods which yield dyes and colouring principles—*Haematoxylon campechianum*, L. (Campeachy wood, logwood), with a red heart-wood from which HÆMATOXYLIN is extracted; *Pterocarpus santalinus*, L. fil. (red sandal-wood), from the heart-wood of which SANTALIN is obtained; *Caesalpinia brasiliensis*, L., and *C. echinata*, Lam. (Brazil wood, Pernambuco wood), with a red heart-wood which supplies BRASILIN; and the Alsage Orange, *Maclura aurantiaca*, Nutt. (yellow Brazil wood), which has a yellow heart-wood from which MORIN is derived. Inorganic substances may also be deposited in the duramen; thus calcium carbonate is found especially in the vessels of the Elm and the Beech, while silicic acid occurs in those of the Teak (*Tectona grandis*).

TYLOSES (Fig. 142) are also instrumental in closing the water-courses of the heart-wood. These are intrusive growths from living cells, which penetrate the cavities of the adjoining tracheal elements during the transition of the sap-wood into heart-wood. In the formation of tyloses the closing membranes of the pits of pitted vessels form bulging ingrowths into the cavities of the vessel. Such ingrowths increase in size until several meet, and so more or less completely close the cavities of the vessels into which they have intruded. The closing membrane of the bordered pits in the heart-wood is pushed to one side, so that the torus presses against the opening of the pit and completely closes it. According to H. MAYR ([125]), resin does not penetrate the walls of wood cells under normal conditions; the wood of Conifers only becomes resinous through the impregnation of the cell walls with resin, after they have become dried up through wounds or other causes. The resin-ducts of Conifers may also be closed by the formation of tyloses.

The **elements of secondary growth** differ in Gymnosperms and Dicotyledons. The vascular strands of Gymnosperms are composed almost exclusively of tracheides (Fig. 141 *A*). These are provided with bordered pits which are situated, for the most part, in their radial walls. The tracheides of the spring-wood (*f*) have larger cavities than those formed later (*s*). Parenchyma is also present in the wood, though in relatively small amount; in some Abietineae resin-passages occur in it (Fig. 141 *h*).

Except in the Gnetaceae, true vessels are not found in the secondary growth, nor in the primary vascular portions, of the bundles of Gymnosperms. The wood produced by the cambium consists of radial rows of tracheides, the number of which is occasionally doubled by the radial division of a cambium cell (Fig. 141 *A*, *a*). The tracheides are often over a millimetre long, much longer than the cambium cells from which they are developed. They attain this length by a subsequent growth, during which their growing ends become pushed in between one another. In addition to the tracheides, small amounts of wood parenchyma are also produced in Gymnosperms by a transverse division of the cambium cells. It is in the parenchymatous cell rows of the wood of Pines, Spruce-Firs, and Larches that the schizogenous resin-ducts are produced (Fig. 141 *A*, *h*). In other Conifers the wood parenchyma consists of simple rows of cells, which afterwards become filled with resin.

Besides tracheides (*t*) and wood parenchyma (*hp*), other elements take part in the composition of the secondary wood of a Dicotyledon; these are the vessels (tracheæ, *g*), and the wood fibres (*h*) (Fig. 145 *A*, *B*). The cells of the wood parenchyma are short and have abundant contents, the woods fibres are thick-walled, long cells with pointed ends. The elements with wider lumens, especially the vessels, are abundant in the spring-wood, in which water conduction is important. The autumn-wood, on the other hand, consists of narrow elements, among which the wood fibres, which contribute to the rigidity of the plant, are numerous. On account of these differences between spring and autumn wood the annual rings are well marked (Fig. 148).

All the elements entering into the formation of the wood of Dicotyledons can be derived from the two classes of tissue already met with in the Gymnosperms, the tracheal tissue and the parenchymatous tissue of the wood. The tracheides and vessels belong to the former class, while under the parenchymatous tissue are included the wood parenchyma, fibrous cells of greater length but with similar contents (Fig. 145 *ef*), and the wood fibres.

The tracheal tissue consists of elements which lose their living contents at an early stage, and in their fully developed condition are in reality only dead cell cavities. In this class are included TRACHEIDES having relatively wide lumina and large bordered pits, and ultimately also spirally thickened walls, which serve as water-carriers (Fig. 145 *A*, *t*) ; VASCULAR TRACHEIDES (*gt*), with similar functions, but with the structure and thickening of vessels ; FIBRE TRACHEIDES (*ft*), with small lumina and pointed ends, having only small, obliquely elongated bordered pits, and, in extreme cases, exercising merely mechanical functions ; and finally TRACHEÆ (*g*), formed by cell fusion, and provided with all the different forms of thickenings by which they are distinguished as annular, spiral, reticulate, or pitted vessels. All vessels function as water-carriers. If they have small lumina and resemble tracheides, they may be distinguished as TRACHEIDAL VESSELS (*tg*) ; if, as is generally the case, they have bordered pits on their lateral walls, they are usually provided with tertiary thickening layers in the form of thin, spiral bands (Fig. 149 *m*). In the parenchymatous tissue of the wood the cells (Fig. 145 *B*) generally retain their living contents, and never develop the true bordered pits with a torus in the closing membrane, which are so characteristic

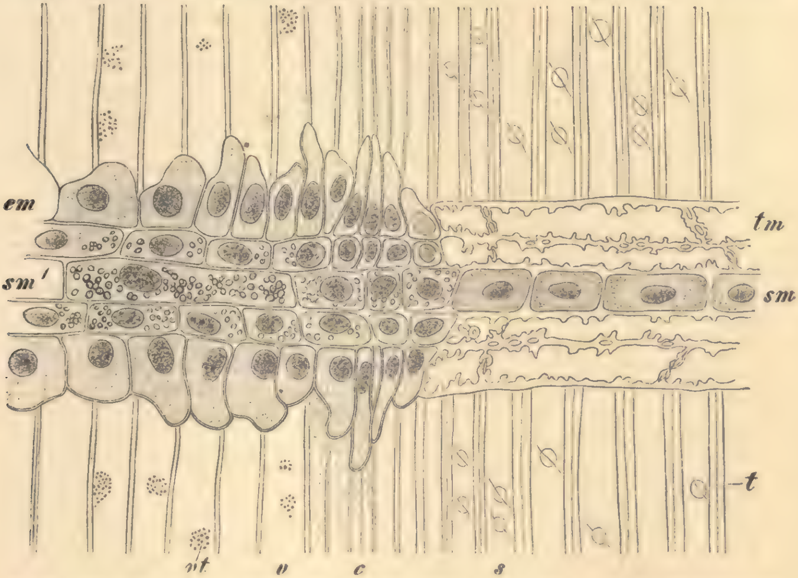


FIG. 143.—Radial section of a Pine stem, at the junction of the wood and bast. *s*, Late tracheides ; *t*, bordered pits ; *c*, cambium ; *v*, sieve-tubes ; *vt*, sieve-pits ; *tm*, tracheidal medullary ray cells ; *sm*, medullary ray cells in the wood, containing starch ; *sm'*, the same, in the bast ; *em*, medullary ray cells, with albuminous contents. (× 240.)

of the water-conducting elements. All tissues of this class may be best derived from wood parenchyma. The wood parenchyma is produced by transverse divisions of the cambium cells, and accordingly consists of rows of cells (*hp*) with transverse division walls, and others obliquely disposed, which correspond to the alternately differently pointed ends of the cambium mother cells. The cells of the wood parenchyma are provided with simple round or elliptical pits, varying in size in different kinds of wood; they generally contain starch, and some of them also take up bye-products, resulting from metabolism, or from the chemical changes taking place within a plant in the processes of its nutrition and growth. The cells having the closest resemblance to those of typical wood parenchyma are the so-called FIBROUS CELLS (*ef*). In their contents, as well as in their wall thickenings, they are similar to the cells of wood parenchyma, but each is formed directly from one entire cambium cell. In their formation, the cells of the cambium tissue become more or less elongated and fibrous. The LIBRIFORM FIBRES or WOOD FIBRES (*h*) have a similar origin, but are even more elongated and have thicker walls, and, at the same time, narrow, obliquely elongated, simple pits. Although the wood fibres may continue living, in the more extremely developed forms (*h*) they lose their living contents. They are then filled with air, and their function is merely mechanical. Under certain conditions, by later transverse divisions, the libriform fibres may become transformed into SEPTATE WOOD FIBRES (*gh*). The transverse septa thus formed remain thin, and form a striking contrast to the more strongly thickened lateral walls. While the tracheal tissues are engaged in providing for the conduction of water, the duty of conducting and storing the products of assimilation, in particular the carbohydrates, is performed by the parenchymatous tissues of the wood. Both forms of tissue, however, aid in maintaining the rigidity of the plant body, and, in their most extreme development, furnish such elements as the fibre tracheides on the one hand, and on the other the empty wood fibres, which are only capable of performing mechanical functions.

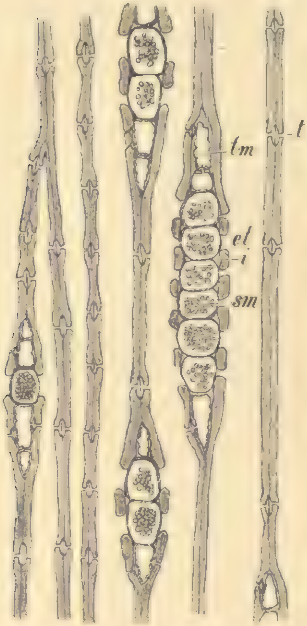


FIG. 144. — Tangential section of the autumn-wood of a Pine. *t*, Bordered pit; *tm*, tracheidal medullary ray cells; *sm*, medullary ray cells containing starch; *et*, pit bordered only on one side; *i*, intercellular space in the medullary ray. (× 240.)

The wood of Dicotyledons is made up of the elements of these two classes of tissue, the tracheal and the parenchymatous, but all the different elements are not necessarily represented in any one kind of wood.

Drimys, a genus belonging to the Magnoliaceae and two genera of the related order Trochodendraceae, are the only Dicotyledons the wood of which is formed of tracheides only. These Dicotyledons closely resemble the Conifers in structure. In numerous Leguminosae, Willows, Poplars, and species of *Ficus*, on the other hand, the tracheal tissues are only represented by vessels, which perform the task of water conduction. In the wood strands of these plants there are also present wood parenchyma and a large proportion of wood fibres. The vessels in climbing plants (lianes) are especially wide.

The distribution of the living elements in the wood strands always bears a distinct relation to the water-courses which they accompany, enclosing them in a more or less complete sheath. The living cells adjoining the tracheal elements are in communication with them by means of one-sided bordered pits. When such pits occur between living cells and tracheal elements the pit cavities are absent on the side of the living cell, but present in the tracheal elements; they differ from the true bordered pits in the absence of a torus on the pit membrane.

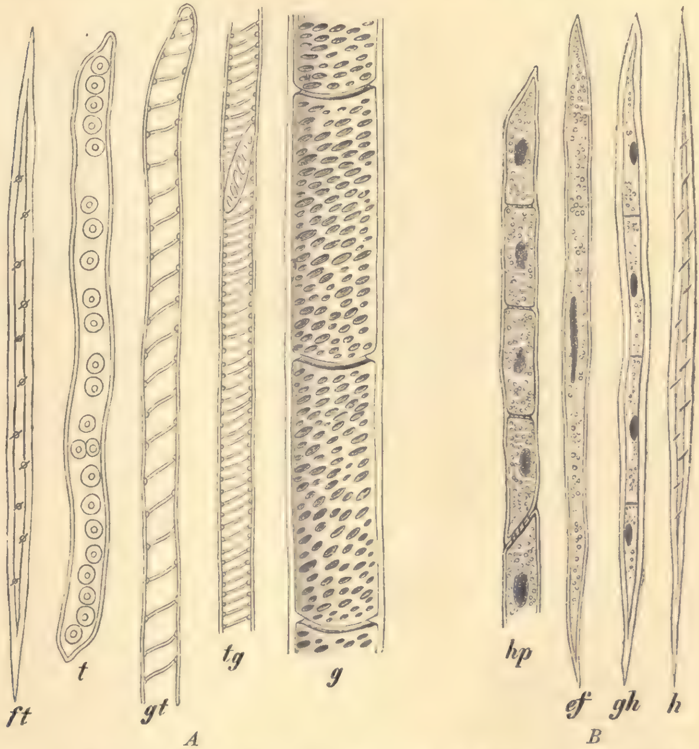


FIG. 145.—*A*, Elements of the tracheal tissue of the wood; diagrammatic. *B*, Elements of the parenchymatous tissue of the wood; diagrammatic. For description see text.

The Elements of the Secondary Phloem in Gymnosperms and woody Dicotyledons are sieve-tubes, or these together with companion cells, bast parenchyma with abundant cell contents, and long narrow bast fibres with strongly thickened walls. The sieve-tubes serve to conduct proteid materials; the companion cells, or in their absence special rows of the bast parenchyma, take up substances from the sieve-tubes; storage and conduction of carbohydrates take place in the parenchyma in which bye-products of metabolism, such as tannins and calcium oxalate, also accumulate.

As in the case of the wood, the elements of the bast may be referred to two forms of tissue, the sieve-tube and the parenchymatous. The former is represented by the sieve-tubes or by these together with companion cells, the parenchymatous portion by the phloem parenchyma and the bast fibres, between which there are intermediate forms of element.

In the bast strands of Gymnosperms, the phloem elements produced by the cambium (Fig. 141 *B*, *c*) consist solely of sieve-tubes, the parenchymatous cells of the bast parenchyma (*p* and *k*), and, in certain cases, of bast fibres. These elements of the bast generally form alternating bands.

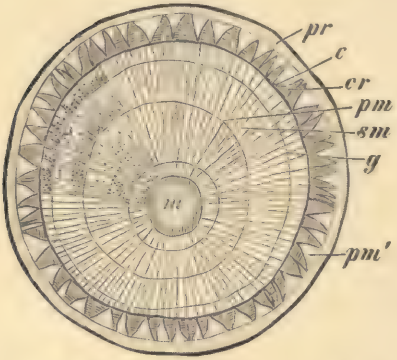


FIG. 146.—Transverse section of a stem of *Tilia ulmifolia*, in the fourth year of its growth. *pr*, Primary cortex; *c*, cambium ring; *cr*, bast; *pm*, primary medullary ray; *pm'*, expanded extremity of a primary medullary ray; *sm*, secondary medullary ray; *g*, limit of third year's wood. (× 6.)

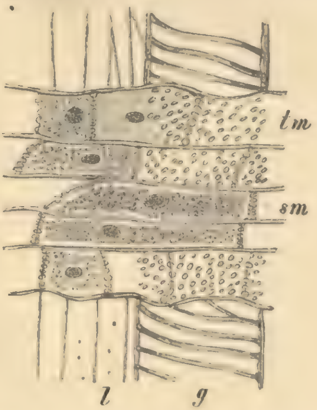


FIG. 147.—A radial section of the wood of *Tilia ulmifolia*, showing a small medullary ray. *g*, Vessel; *l*, wood fibres; *tm*, medullary ray cells in communication with the water-courses by means of pits; *sm*, conducting cells of the medullary ray. (× 240.)

The Araucarieae, Taxineae, and Cupressineae have definite, vertical rows of bast parenchyma cells which take the place of the companion cells wanting in these plants. At a certain distance from the cambium the sieve-plates become overlaid by callus. During the vegetative period following their development, the sieve-tubes become empty and compressed together (Fig. 141 *B*, *cr*). The rows of bast parenchyma cells containing albuminous substances, which are found in some Conifers, undergo disorganisation at the same time as the adjacent sieve-tubes; the bast parenchyma cells which contain starch, on the other hand, continue living for years, and even increase in size, while the sieve-tubes become compressed.

The elements of the phloem tissue included in the bast strands of woody Dicotyledons (Fig. 150) are represented by SIEVE-TUBES (*v*) and COMPANION CELLS (*c*). To the parenchymatous tissues of the bast belong BAST PARENCHYMA (*p*), BAST FIBRES (*l*) and transitional forms between them.

The bast fibres, like the fibres of the wood, may occur in an unthickened form as FIBROUS CELLS, either with or without living contents, or they may be filled with starch, or finally may become septate.

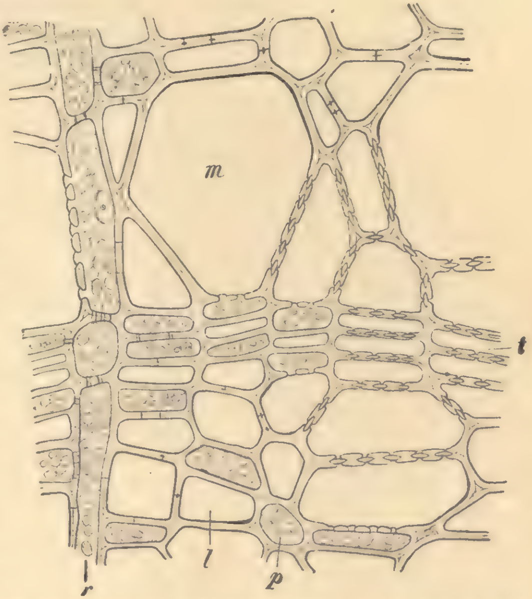


FIG. 148.—Portion of a transverse section of the wood of *Tilia ulmifolia*. *m*, Large pitted vessel; *t*, tracheides; *l*, wood fibre; *p*, wood parenchyma; *r*, medullary ray. (× 540.)

The elements of the bast of Dicotyledons frequently exhibit a great regularity in their arrangement. Thus in the Lime (Fig. 150) there is a regular alternation of sieve-tubes (*v*) and companion cells (*c*), bast parenchyma containing starch (*p*) and crystals (*k*), tangentially flattened bast parenchyma (*p*), and then another zone of sieve-tubes. The sieve-tubes of Dicotyledons as of Gymnosperms only remain functional for a short time, after which they become empty and crushed. The companion cells, which are sister cells of the sieve-tubes, undergo the same fate. The starch-containing parenchyma, on the other hand, may remain for years unaltered. The differences in the appearance of the bast of dicotyledonous trees are due to the greater or less diameter of the sieve-tubes, the presence or absence of bast fibres, and the arrangement of the various elements.

The **Medullary Rays** of the Gymnosperms (Fig. 139 *ms*) and woody Dicotyledons (Fig. 146 *pm*, *sm*) form radial bands, composed wholly or in part of parenchymatous elements. Their function is to supply the cambium and wood with the products formed in the leaves and conveyed away by the bast; they also conduct water outwards from the xylem. The medullary rays in this way link together by radial bands of living cells the protoplasm-containing elements of the bast and wood, thus uniting all the separate living tissues of the stem. The medullary rays are in turn accompanied or, if many-layered, traversed by intercellular spaces filled with air. These, beginning in the periphery of the stem, penetrate the cambium and communicate with all the intercellular spaces throughout the living elements of the wood and bast. All the living elements are kept in communication with the atmosphere by means of the intercellular spaces of the medullary rays, and the necessary interchange of gases is thus rendered possible.

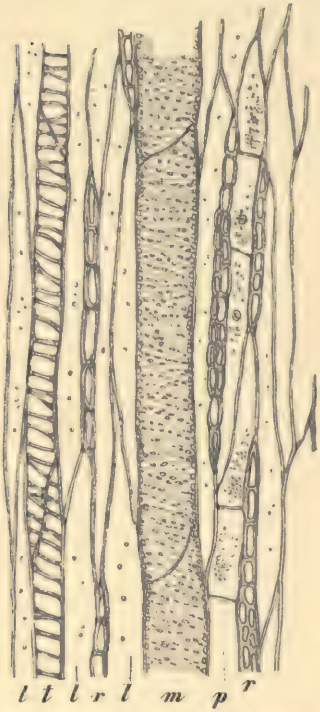


FIG. 149.—Tangential section of the wood of *Tilia ulmifolia*. *m*. Pitted vessel; *t*, spiral tracheides; *p*, wood parenchyma; *l*, wood fibres; *r*, medullary rays. (× 160.)

The substances contained in the parts of the medullary rays within the wood, chiefly consisting of starch, tannins, resin, and crystals, are essentially the same as those in the wood parenchyma. In the medullary rays of certain Gymnosperms, particularly in the Pine, single rows of cells, without living contents and situated usually at the margin of the medullary bands, become tracheidal in structure (Figs. 143, 144 *tm*), and united with one another and with the tracheides by means of bordered pits. Their purpose is to facilitate the transfer of water radially between the tracheides. In other Conifers, where such tracheidal elements are not found in the medullary rays, bordered pits are developed in the tangential walls of the tracheides of the autumn-wood, and by means of them the transfer of water in a radial direction is effected. The living cells of the medullary rays of the wood bear the same relation to the water-carriers as does the wood parenchyma, and like them are connected with the water-conducting elements by means of bordered pits on one side of the cell wall. They take up water from them and give it out again, as it may be needed, to other living cells; on the other hand, in the spring, at the beginning of the season of growth, they press into the water-courses the products of assimilation, in particular glucose and small quantities of albuminates, in order that these substances may be transferred in the quickest way to the points of consumption. Accordingly, during the winter and in the beginning of spring, sugar and albumen may be detected in the tracheal elements (126), and may then be obtained from the watery sap of "bleeding" trees, or from artificial borings or incisions, particularly in such trees as the Maple, Birch, and Hornbeam. In the wood of Dicotyledons it is usually only special rows of the medullary ray cells which stand in such close relation with the tracheal tissues. In these special rows, generally on the margins of the medullary rays, the cells are elongated vertically, and on that account have been distinguished as VERTICAL MEDULLARY RAY CELLS. The other cells, or those of the middle layers of the medullary bands, on the other hand, are called HORIZONTAL MEDULLARY RAY CELLS; they are narrower and more elongated radially (127). These have no especial connection with the tracheal elements, but are designed for conducting and storing assimilated substances. Within the bast zone the medullary rays of Dicotyledons have a simpler structure than in the wood. It is evident, not only from the pits between the cells of the medullary rays and the bast parenchyma, but also from the similar relations in Dicotyledons between the medullary ray cells and the companion cells of the sieve-tubes, that the function of the cells of the medullary rays in the phloem is to take up substances passing down the bast strands.

In the Pine and other Abietineae, whose bast parenchyma is devoid of cells functioning as conductors of albuminous matter, their place is taken in this respect by rows of medullary ray cells (Fig. 143 *cm*). These maintain an intimate connection with the sieve-tubes by means of sieve-pits. They lose their contents in the same manner as the sieve-tubes, and, like them, become compressed and disorganised. On the other hand, the cells of the medullary rays, which contain starch, like the similar cells of the bast parenchyma, increase in size, and continue living for years.

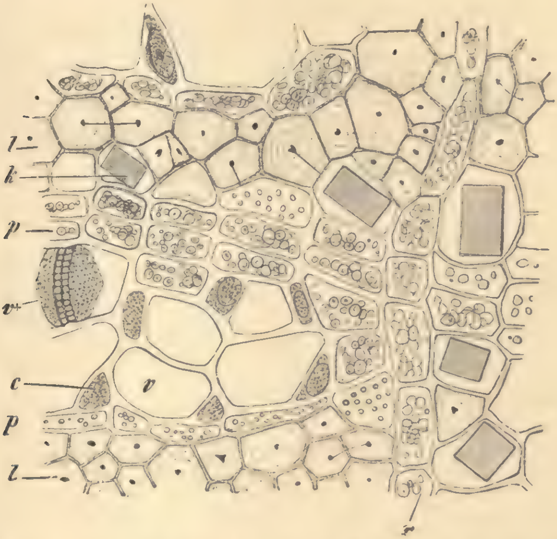


FIG. 150.—Portion of a transverse section of the bast of *Tilia ulmifolia*. *v*, Sieve-tubes; v^*, sieve-plate; *c*, companion cells; *k*, cells of bast parenchyma containing crystals; *p*, bast parenchyma; *l*, bast fibres; *r*, medullary ray. (× 540.)

The width and height of the medullary rays may be more easily determined from tangential than from radial sections. In such tangential sections the medullary rays appear spindle-shaped (Figs. 144, 149). With few exceptions, as in the Oak and Beech, the medullary rays are of relatively small size. The Oak, in addition to numerous small medullary rays, has other larger rays which may be as much as a millimetre broad and a decimetre high. In the Poplar, Willow, and Box the medullary rays are so extremely small that they are scarcely visible, even with the aid of a magnifying glass. The height of the broad primary rays of many lianes, on the other hand, may be equal to that of a whole internode. In certain Conifers, resin-ducts occur not only in the wood, but also in the broader medullary rays. These radial resin-ducts are in communication with the vertical ducts. It is due to this fact that such a large amount of resin exudes from wounds in Pine or Fir trees.

Secondary Thickening of the Root in Gymnosperms and Dicotyledons.—The ROOTS of Gymnosperms and Dicotyledons, in which the stems increase in thickness, show a similar GROWTH IN THICKNESS ([128]). When secondary growth begins in a root with its xylem and phloem strands alternating with each other (Figs. 124, 131), layers of cambium arise on the inside of the phloem strands, through the division of the fundamental tissue; these give off wood elements towards the centre of the root, and bast towards the periphery. These cambium layers soon meet in the pericycle, just outside the xylem strands, and so form a complete cambial ring. In Fig. 151 *A*, this process is diagrammatically represented. As a result of the activity of its cells the cambium ring soon loses its sinuous form, and becomes circular. In front of the primary vascular strands (g'), the cambium produces medullary ray tissue, and this constitutes the broadest medullary rays which lead inwards to the strands of primary xylem (Fig. 151 *B*). A cross-section of such a root, in which the secondary growth has continued for some years, can scarcely be distinguished from a cross-section of a stem. By careful examination, however, the presence of primary xylem in the centre of the root can be discovered, and its nature thus determined. The wood of the root is also more porous than in the stem, and bears a close resemblance to spring-wood. On account of this lack of differentiation in the wood, the annual rings of growth are less distinctly defined in roots than in stems.

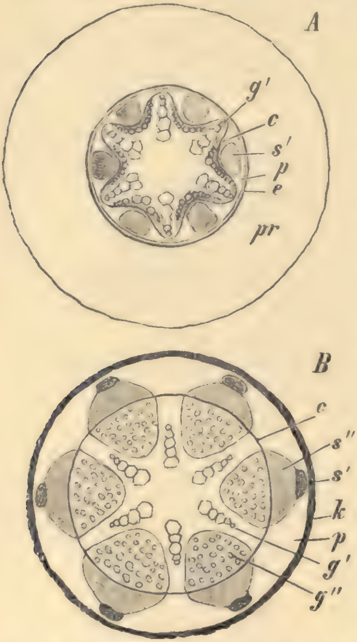


FIG. 151.—Diagrammatic representation of the growth in thickness of a dicotyledonous root. *pr*, Primary cortex; *c*, cambium ring; *g'*, primary vascular strand; *s'*, primary phloem strand; *p*, pericycle; *e*, endodermis; *g''*, secondary wood; *s''*, secondary bast; *k*, periderm.

In the root and its branches, as in the stem, the annual zones of secondary growth become less numerous on approaching the growing points (Fig. 140).

Anomalous forms of Growth in Thickness ([129]).—Extraordinary deviations from the usual type of secondary growth are afforded by some stems and roots of Gymnosperms and Dicotyledons. Among the Gymnosperms in the Cycadaceae and certain species of *Gnetum*, in the Chenopodiaceae, Amarantaceae, Nyctaginaceae, Phytolaccaceae, and other families of Dicotyledons, the cambium which has been formed in the ordinary manner soon loses its function, and a new cambium ring is developed external to the bast zone, for the most part in the pericycle, or in a tissue derived from it. This cambium ring forms wood on the inside and bast on the outside, with the accompanying medullary rays. It then ceases to divide, and a new ring takes its place. This process is repeated, and ultimately leads to the formation of concentric rings of wood and bast, which, in cross-sections of the sugar-beet, may be distinguished with the naked eye. These concentric zones may be still more plainly seen in a cross-section of *Mucuna altissima* (Fig. 152), a liane belonging to the order Papilionaceae. The stem shows in this case an inner axis of wood (1) surrounded by a zone of bast (1*) ; next follows a cylinder of wood (2) and bast (2*), and finally a third (3, 3*) in process of formation in the pericycle.

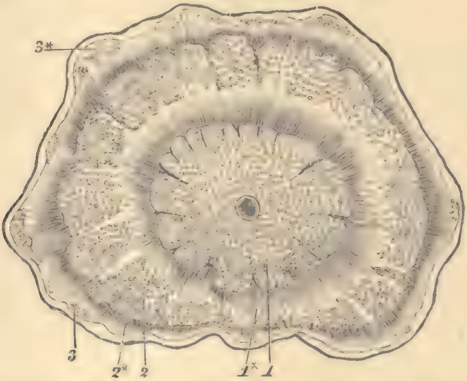


FIG. 152.—Transverse section of the stem of *Mucuna altissima*. 1, 2, 3. Successively formed zones of wood ; 1*, 2*, 3*, successively formed zones of bast. (⅔ nat. size.)

An extraordinary appearance is exhibited by cross-sections of stems, which show several separate wood cylinders (Fig. 153). Such a structure is peculiar to various tropical lianes of the genera *Serjania* and *Paullinia* belonging to the family Sapindaceae. This anomalous condition arises from the unusual position of the primary vascular bundles, which are not arranged in a circle but form a deeply lobed ring ; so that, by the development of interfascicular cambium, the cambium of each lobe is united into a separate cambium ring. Each of these rings, independently of the others, then gives rise to wood and bast (Fig. 153). A very peculiar structure is exhibited by many lianes of the Bignoniaceae, the wood of which is cleft by radially projecting masses of bast (Fig. 154). The primary stem of the Bignoniaceae shows the ordinary circular arrangement of the vascular bundles. Wood and bast are at first produced from the cambium ring in the usual manner, and an inner, normal wood cylinder of AXIAL WOOD is formed. Such normally formed axial wood cylinders are common to many, otherwise abnormally developed lianes. The cambium ring of the Bignoniaceae, after performing for a time its normal functions, begins, at certain points, to give off internally only a very small quantity of wood, and externally a correspondingly large amount of bast. As a result of this, deep wedges of irregularly widening bast project into the outer so-called PERIAXIAL WOOD (Fig. 154). The originally complete cambium becomes thereby broken into longitudinal bands, which are broader in front of the projecting wood than at the apices of the bast wedges. As the periaxial wood is always developed from the inside, and the wedges of bast from the outside of their respective cambium bands, they extend past each other without forming any lateral connection.

The Formation of Knots.—The knots or streaks which add so greatly to the technical value of certain woods depend on an unusually bent or interwoven course of the elements of the wood. Their origin is due to the stimulus of wounding, to the effects of parasites, the pressure exerted by lateral branches which are increasing in thickness, or to altered cambial activity. Larger knots are produced by the origin of numerous adventitious buds, especially after wounding; a finer marking by the widening of the medullary rays, which may then appear circular in tangential section, and influence the course of the adjacent elements of the xylem (130).

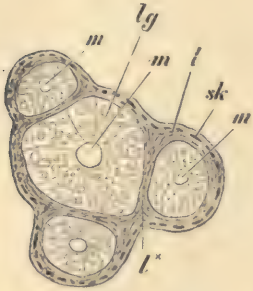


FIG. 153.—Transverse section of the stem of *Serjania Laruotteana*. *sk*, Part of the ruptured sclerenchymatous ring of the pericycle; *l* and *l**, bast zones; *lg*, wood; *m*, medulla. (× 2.)

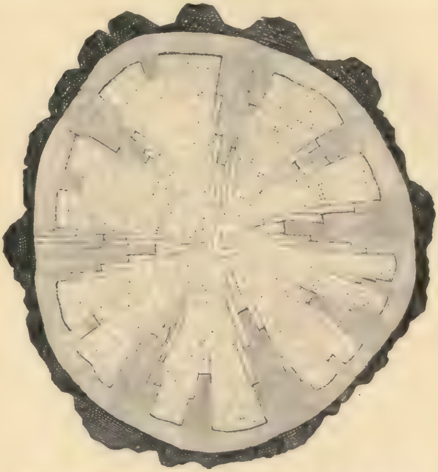


FIG. 154.—Transverse section of the stem of one of the Bignoniaceae. (Nat. size.)

Secondary Growth of Monocotyledons.—There are certain monocotyledonous plant families and genera, especially *Dracaena*, *Yucca*, *Aloe*, and the Dioscoreaceae, in the stems and roots of which a cambium ring is developed. As in such cases, the cambium ring generally arises in the pericycle, outside the scattered vascular bundles and from the fundamental tissue, it is a secondary meristem; it does not, as in Dicotyledons and Gymnosperms, produce continuously wood and bast in opposite directions, but, instead, only new tissue to the inner side. This later becomes differentiated into closed vascular bundles embedded in a thick-walled parenchymatous ground tissue.

The cambial ring in these cases is only active to one side (131). and its initial cells are replaced from the cells of the ground tissue on the outer side of the ring (p. 128).

At a later period the cambial ring commences to form cells to the outer side which increase the thickness of the cortex as a thin-walled, parenchymatous ground tissue (Fig. 155). When the cambium has thus become active on both sides it presents the appearance of a single initial layer.

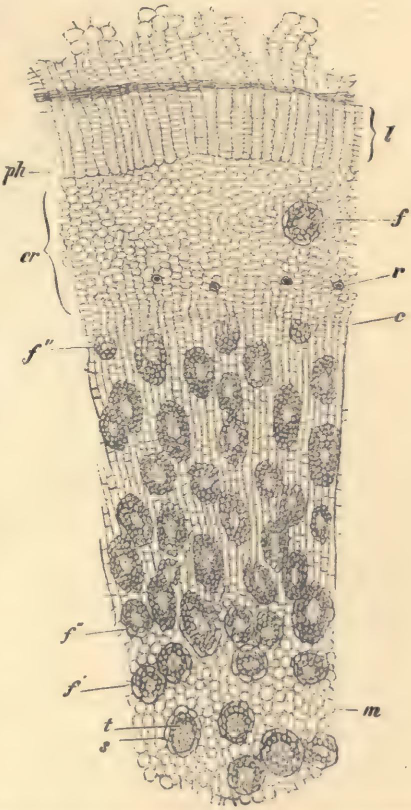


Fig. 155.—Transverse section of the stem of *Cordyline* (*Dracaena*) *rubra*. f', Primary vascular bundles; f'', secondary vascular bundles: f''', leaf-trace bundle within the primary cortex; *m*, parenchymatous fundamental tissue; *s*, bundle-sheath; *t*, tracheides; *c*, cambium ring; *cr*, cortex, the outer portion being primary, the inner secondary cortex; *ph*, cork cambium; *l*, cork; *r*, bundles of raphides. (× 30.)

As shown in the diagram (Fig. 156) the growth in thickness of a Monocotyledon differs essentially from that of a Gymnosperm or Dicotyledon represented diagrammatically in Fig. 140. The stem of a *Dracaena* on which the diagram is based is represented as unbranched. Its primary central cylinder (*pc*) increases in diameter as the stem grows in length, and thus forms an inverted cone. It is surrounded by the zones of secondary growth, the amount of which diminishes on passing towards the growing point. The secondary growth of the stem is continuous with that of the roots.

Secondary Growth of Leaves (132) is always very slight, and is confined to a few Coniferae and Dicotyledons with evergreen leaves. The increase in thickness is due to the presence of a fascicular cambium. This produces little or no xylem, the new elements being mostly added to the phloem. Any elements formed on the side next the xylem are water-conducting, while those adjoining the phloem mostly become sieve-tubes.

Periderm (133).—It is very seldom that the epidermis, by the division of its own cells, is in a condition to keep pace for any length of time with the increasing dimensions of the stem. This, however, is the case with the Mistletoe (*Viscum album*), the number of epidermal cells of which is continually augmented by the formation of new lateral walls, and new cuticular layers are formed where the old cuticle becomes ruptured. On older portions of the stem, however, thickening layers form in single epidermal cells or groups of epidermal cells, and at the same spots similarly thickened cortical cells are developed. The epidermal cells thus cut off die, and the original epidermis is more or less completely replaced on such old regions of the stem. In the great majority of plants in which the epidermal layer persists for years it is able to meet the demands made upon it by the growth in thickness of the stem without the assistance of the underlying cortex. The stems of one of the Maples (*Acer striatum*), even when a foot or more in thickness and over forty years old, remain covered with a living, growing, epidermal layer. The striations to which the specific name of this plant refers are caused by a white wax exuding from splits in the outer walls. As a rule, however, the epidermis on stems which grow in thickness becomes stretched and finally ruptured. The tissue of the primary cortex and of the bast by the expansion and division of its cells, can accommodate itself more easily than the epidermis to the increased dimensions of the stem, arising from the growth in thickness of the central cylinder. This process of accommodation is particularly noticeable in the primary medullary rays (Fig. 146, *pm'*) between the primary phloem. The formation of the PERIDERM generally begins during the first vegetative period, after the secondary growth has reached a certain stage. The commencement of its formation is indicated by the brown colour of the external surface of the stem, which remains green so long as the epidermis continues alive. The formation of periderm usually occurs at a later period in those plants which have a persisting epidermis; it is practically wanting only in the species of Mistletoe. The periderm is derived from a secondary meristem, termed the CORK CAMBIUM or PHELLOGEN. This phellogen may arise, in the epidermis, in a deeper layer of cells of the primary cortex, or even in the pericycle itself.

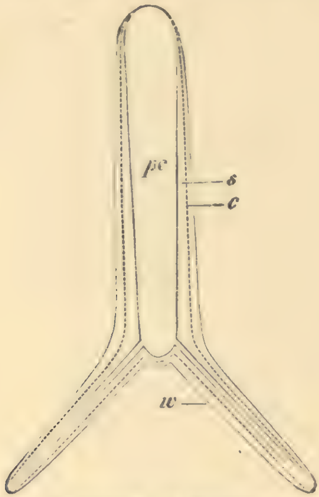


FIG. 156.—Diagram of the secondary growth of the stem and root of *Dracaena*. *pc*, Central cylinder; *s*, secondary tissue; *c*, cambium indicated by a dotted line; *w*, root. (Adapted from SCHOUTE.)

The phellogen (124) is as a rule a cambium with a persisting initial layer from which cork-cells are produced to the outside and phelloderm to the inside.

The production of cork-cells is usually greater than that of phelloderm. If the phelloderm forms only cork-cells the initial cells are often used up in the process, and are then replaced from the adjoining ground tissue (p. 128). This is found among Monocotyledons and also in some Dicotyledons, *e.g. Valeriana officinalis.*

The young cork-cells usually have a tabular shape, fit closely together without intercellular spaces, and possess suberised, secondary, thickening layers. The cork cells usually possess brown walls. They may be thin (Fig. 155 *l*) or thick, frequently thickened on one side (Fig. 157), and occasionally to such an extent that they are known as stone cork. Thin-walled cork-cells usually contain air; those with thickened walls frequently have reddish-brown cell contents (phlobaphene) consisting mainly of tannins and products derived from them. The cork tissue frequently shows an alternation of narrow thick-walled with thin-walled and larger cells. These layers mark annual growths. Even thin corky walls, being impermeable to water, prevent the loss of moisture by transpiration. Thicker layers of cork afford mechanical protection and hinder the invasion of the plant by parasites.

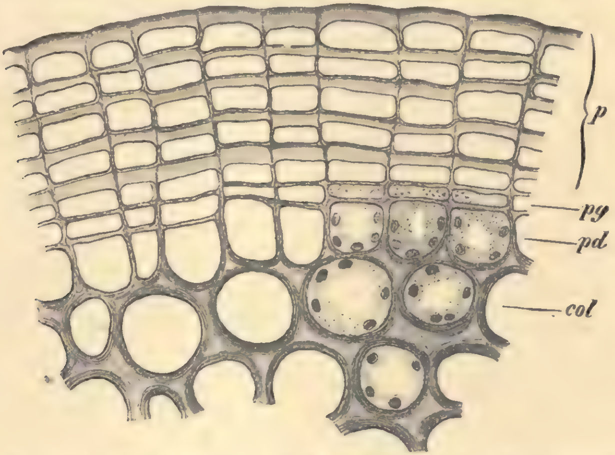


FIG. 157.—Transverse section of the outer part of a one-year-old twig of *Pyrus communis* made in autumn. It shows the commencement of the formation of the periderm. *p*, cork; *pg*, phellogen; *pd*, phelloderm; *col*, collenchyma. The cork-cells have their outer walls thickened and have brown dead contents. (× 500.)

The phelloderm formed to the inner side of the phellogen in many cases, such as the Currant, attains a considerable thickness. Its cells retain their living protoplasm, and usually contain chloroplasts.

They ultimately become rounded off, so that intercellular spaces are formed between them and serve to increase the thickness of the living cortex. The term periderm includes both cork and phelloderm.

The cork of the Cork-oak (*Quercus Suber*) is formed of broad layers of soft large cells, alternating with narrow layers of thinner cells, which mark the limit of the annual growth. This may be seen in bottle-corks. The first, spontaneously developed cork of the Cork-oak is stripped off, whereupon a new phellogen is formed in the deeper-lying tissue. The cork thus produced is removed every six or eight years, and furnishes the cork of economic value.

In many cases the phellogen takes its origin in the epidermis (Fig. 157 *pg*). This is the case in the Willow, in all Pomaceae, and in a number of other woody plants. The epidermal cells become divided into outer and inner cells, the latter of which assume the function of a phellogen. More frequently the phellogen develops from the layer of cells next adjoining the epidermis, as, for example, in the Elder (*Sambucus nigra*), where it takes its origin from the outermost layer of collenchyma (Fig. 158, *ph*). The epidermis in this case covers the developing layer of cork.

True cork is confined to *Ophioglossum* among the Cryptogams. The fleshy stipules of the Marattiaceae are covered with a brown layer arising by the irregular division of sub-epidermal cells ; the walls of this tissue are humified and it may be termed pseudo-periderm (134).

Bark.—All tissues external to the phellogen are cut off from food supplies, and consequently die. When the first cork layer has its origin deep within the stem, a BARK of considerable thickness is formed through the ensuing death of the peripheral tissues. If the cork layer formed by the phellogen be thin, the stem has a smooth surface, as in the Beech ; if it produces thicker cork layers, the surface of the stem appears rough and full of fissures, as is the case in the Cork-oak. The primary phellogen generally ceases its activity after a short time, and another deeper-lying phellogen is formed. After a time this new phellogen discontinues its functions, and another (Fig. 159) is developed, as in the case of *Quercus sessiliflora*, until ultimately the phellogen comes to be formed in secondary bast parenchyma instead of in the primary tissue. That portion of the bast cut off by the periderm loses its nutritive contents and only retains waste products. If the layers of the secondary periderm constitute only arcs of the stem circumference, the bark will be thrown off in scales, as in the SCALY BARK of the Pine and Plane tree ; if, on the contrary, the periderm layers form complete concentric rings, then hollow cylinders of the cortical tissues are transformed into the so-called RINGED BARK, such as is found in the Grape-vine, Cherry, Clematis, and Honeysuckle. Bark which is not easily detached becomes cracked by the continued growth in thickness of the stem, and has then the furrowed appearance so characteristic of the majority of old tree-trunks. The usual brown or red colour of bark, just as in similarly coloured heart-wood, is occasioned by the presence of tannins, to the preservative qualities of which is due the great resistance of bark to the action of destructive agencies. The peculiar white colour of Birch-bark is caused by the presence of betulin (birch-resin) in the cells.

In roots which grow in thickness the phellogen usually develops in the pericycle (Fig. 151 *B*, *k*), and in consequence of this the primary cortex of the roots dies and peels off. The succeeding phellogen layers are formed in exactly the same way in the root as in the stem.

Lenticels (^{135}).—In most woody plants, particularly in Dicotyledons, cortical pores, or LENTICELS (Fig. 158), make their appearance simultaneously with the formation of periderm. The lenticels take their origin in a phellogen layer (*pl*) which, in the case of peripheral cork formation, almost always develops directly under the stomata. The phellogen, from which the lenticels arise, unlike the cork phellogen, does not form cork cells, but a lenticel tissue composed of COMPLEMENTARY CELLS (*l*) with intercellular spaces between them. On the inside, however, a phelloderm is regularly derived from the phellogen. The complementary cells press the epidermis outwards and finally rupture it. Where the complementary cells are only loosely united, intermediate bands or closing layers are developed from the phellogen alternately with the layers of looser tissue; the closing layers become eventually ruptured. The complementary cells are as a rule not suberised, those of the closing bands are corky and lignified. The cork-forming phellogen joins the phellogen of the lenticels at its margins. In cases where the cork is more deeply seated in the inner tissue, the lenticels begin their development at a corresponding depth from the layer of phellogen. Lenticels serve to maintain the

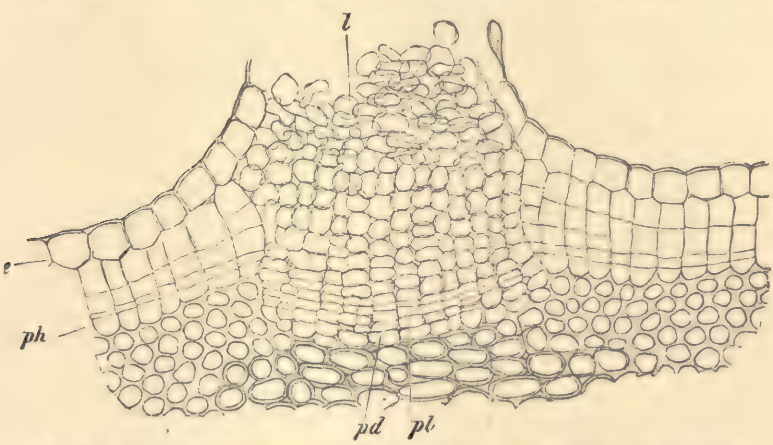


FIG. 158.—Transverse section of a lenticel of *Sambucus nigra*. *e*, Epidermis; *ph*, phellogen; *l*, complementary cells; *pl*, phellogen of the lenticel; *pd*, phelloderm. (× 90.)

gaseous interchange between the outside air and the gases present in the intercellular spaces of the plant.

Certain aerial roots such as those of the Orchids and the respiratory roots of swamp plants possess lenticels the structure of which deviates more or less from the usual type; these are termed pneumathodes.

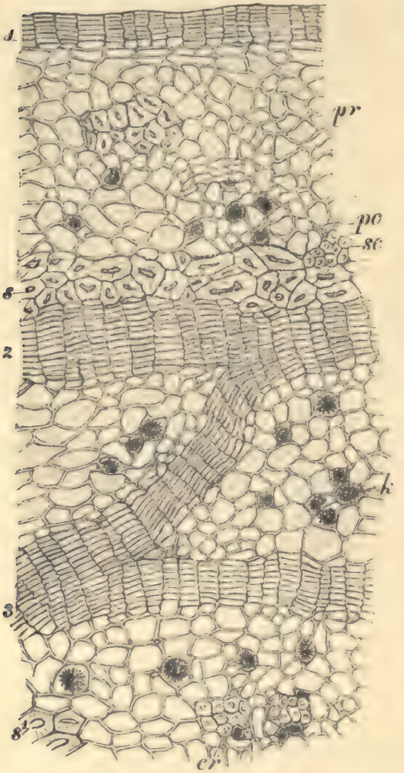


FIG. 159.—Transverse section of the peripheral tissues of the stem of *Quercus sessiliflora*. 1, 2, 3, Successively formed layers of cork; *pr*, primary cortex, modified by subsequent growth; internally to *pc*, pericycle; *sc*, sclerenchymatous fibres, from the ruptured ring of sclerenchymatous fibres of the pericycle; *s*, subsequently formed sclereids: *s'*, sclereids, of secondary growth; *cr*, bast fibres with accompanying crystal cells; *k*, cells, with aggregate crystals. All the tissue external to the innermost layer of cork is dead and discoloured, and has become transformed into bark. (× 225.)

Absciss Layers.—The fall of the leaves of woody plants (136) is brought about by means of a layer of parenchymatous tissue which is formed at the base of the leaf-stalk shortly before the leaf-fall. The cells of this tissue separate from one another owing to their middle lamellæ becoming mucilaginous. Within this absciss layer all prosenchymatous elements of the petiole are greatly reduced; only the tracheal elements are lignified, and these are broken through when the leaf separates. The protection of the leaf-scar is effected in the first place by the lignification and suberisation of the walls of the exposed cells, and later by the formation of a layer of cork continuous with the periderm covering the stem. The ends of the tracheal elements in the scar become occluded by wound-gum or thylosis or by both; the ends of the sieve-tubes become compressed and lignified. The leaflets of compound leaves usually become separated from the rhachis by absciss layers. Herbaceous plants exhibit as a rule no definite leaf-fall (137).

Healing of Wounds (138).—Lost portions of tissue are in the lower plants frequently regenerated directly, while this only occurs to a very limited extent in more highly organised plants (139). In the latter regeneration is limited to the periderm, and in a few instances to parts of the vascular bundles. In the simplest cases among land plants the wounded cells die and become brown and dry, while the walls of the underlying uninjured cells become lignified. The protection of wounded surfaces takes place in this way in the Cryptogams and when the wound is very small in Phanerogams. In the case of larger wounds in the latter a cork-cambium, forming wound-cork, develops below the lignified cells. This cork is lignified as well as suberised ([140]). Suberisation of the walls of the cells immediately underlying the wound may precede the formation of cork. This occurs in seed potatoes which are divided up before planting and left one or two days exposed to the air. On this depends their resistance to injurious influences in the soil ([141]). Secretory receptacles in wounds become closed by thyloses. Laticiferous elements are first closed by the coagulation of the latex at the point of wounding and below this a cell-wall is formed ([142]). In woody plants a so-called CALLUS is formed by the active growth of the living cells bordering on the wound. These swollen growths close together over the wound, and by the suberisation of their cell-walls provide a sufficient protection. Generally, however, a cork-forming phellogen arises in the periphery of the callus. In stems of Gymnosperms and Dicotyledons, wounds which extend into the wood become surrounded and finally overcapped by an outgrowth of tissue arising from the exposed cambium. While the callus tissue is still in process of gradually overgrowing the wounded surface, an outer protective covering of cork is developed; at the same time a new cambium is formed within the callus, through a differentiation of an inner layer of cells, continuous with the cambium of the stem. When the margins of the overgrowing callus tissue ultimately meet and close together over the wound, the edges of its cambium unite and form a complete cambial layer, continuing the cambium of the stem over the surface of the wound. The wood formed by this new cambium never coalesces with the old wood. Accordingly, marks cut deep enough to penetrate the wood are merely covered over by the new wood, and may afterwards be found within the stem. In like manner, the ends of severed branches may in time become so completely overgrown as to be concealed from view. The growing points of adventitious shoots often arise in such masses of callus. As the wood produced over wounds differs in structure from normal wood, it has been distinguished as CALLUS WOOD. It consists at first of almost isodiametrical cells, which are, however, eventually followed by more elongated cell forms. At the base of cut-off portions of plants which are used as cuttings a callus formation which according to the kind of plant is more or less active, takes place. In extreme cases the callus forms projecting masses within which the rudiments of adventitious roots arise.

Regeneration.—Lost parts of the body of Fungi and Algae are often replaced, a direct regeneration thus taking place. In more highly organised plants such a proceeding is extremely rare. It occurs most readily in embryonic organs, such as growing points, when portions have been lost, and is most often found in seedlings. Thus in seedling plants of *Cyclamen* even a severed leaf-blade has been found to be replaced. As a rule, however, when regeneration processes are requisite in higher plants and the necessary preformed organs are not present in a resting or latent condition, the older tissues return to the embryonic condition and give rise to new growing points of shoots (143). That this is a provision for the indirect replacement of lost parts is confirmed by the fact that direct regeneration is far more frequent among animals than plants.

The Phylogeny of the Internal Structure

The phylogenetic differentiation in the internal structure of a plant does not altogether coincide with the progress of its external segmentation. Even unicellular plants of the Siphoneae may exhibit a high degree of external differentiation; thus the unicellular Alga, *Caulerpa* (Fig. 295), has developed appendages having outwardly the forms of leaf, stem, and root. Similarly, the Red Seaweed, *Hydrolapathum* (Fig. 9), although composed almost entirely of one form of cells, bears in its external segmentation a resemblance to one of the most highly organised plants. The internal differentiation of this Alga has only advanced so far, that the outer cells containing the red chloroplasts form an assimilating tissue of isodiametrical cells, while the internal colourless and

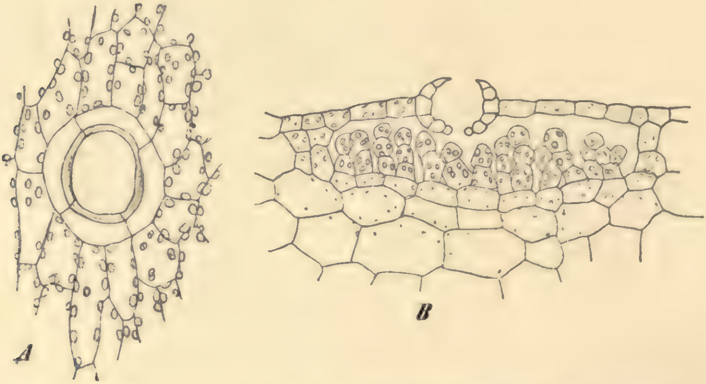


FIG. 160.—Surface view and transverse section of the thallus of *Marchantia polymorpha*. In *A*, an air-pore, as seen from above; in *B*, as seen in cross-section. (× 240.)

more elongated cells function as a conducting tissue. The relatively highest degree of internal development found in the Algae is attained by the Laminariae. In their stem-like axis, which may have a considerable thickness, the external tissues frequently contain canals filled with mucilaginous matter; while internally are found rows of cells resembling sieve-tubes (108). The axes themselves grow in thickness through the continuous division of the cells of one or more of the outer cell layers. A kind of cortical tissue is formed as a result of this growth which exhibits concentric layers; the innermost cells gradually elongate and pass over into the so-called medulla. In the larger Fungi internal differentiation is the result of the more or less intimate union of the intertwining hyphæ. In extreme cases the hyphæ forming the body of the Fungus may be so closely woven together as to give, in a cross-section, the impression of a parenchymatous tissue (Figs. 106, 107), in which, on the subsequent thickening of the cell walls, the pits in adjoining hyphæ coincide. In the fructifications of many of the Hymenomycetes and Gasteromycetes, some of the longer and more swollen hyphæ contain a homogeneous or cloudy, highly refractive, and, in some instances, coloured substance, and appear, accordingly, to serve as a special tissue for the purpose of conduction. A marked advance in the differentiation into different tissue systems is first apparent in the Bryophytes, but even in them the formation of an epidermis distinct from the fundamental tissue is exceptional. In the thallus of the Marchantieae and on the spore capsules of the Anthocerotaceae and Bryineae, the external layer of cells become more or less sharply defined from the underlying tissues. In the Marchantieae (Fig. 160) this outer layer is pierced by openings which have been termed breathing-pores, but these have a different origin from the stomata of higher plants. They are rather, as LEITGEB (144) has shown, openings into cavities, which have arisen through the overarching of certain portions of the surface by other

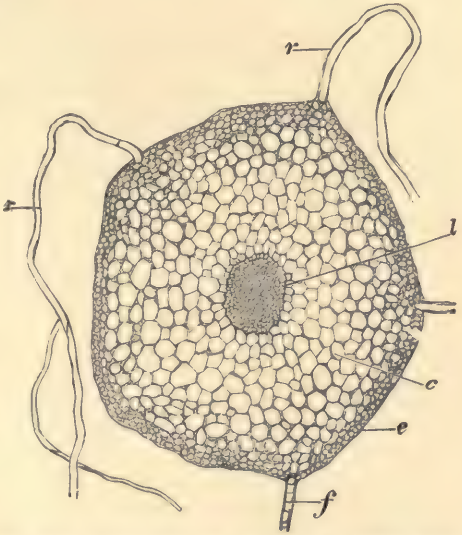


FIG. 161.—Transverse section of the stem of *Mnium undulatum*. *l*, Conducting-bundle; *c*, cortex; *e*, peripheral cell layer of cortex; *f*, part of leaf; *r*, rhizoids. (× 90.)

more rapidly growing portions. In the Anthocerotaceae and Bryineae, on the other hand, stomata similar in structure to those of the Pteridophytes and Phanerogams are found in the outer cell layer of the spore capsules. It would seem, however, that these stomata of the Bryineae are probably not homologous with those of higher plants. It is more reasonable to regard them as merely analogous formations, such as from internal causes so often occur in the evolution of organs. In the stems of many of the Bryineae there is also developed a simple form of conducting bundle (Fig. 161); and the many-layered midrib of the single-layered leaf lamina is also traversed by a conducting strand. In spite of their more advanced differentiation, the Bryophytes may still be included, just as they were originally in 1813 by AUGUSTE PYRAME DE CANDOLLE (145), in his classification of the vegetable kingdom according to the natural system, with the other lower Cryptogams in the class of CELLULAR PLANTS, as distinguished from the VASCULAR PLANTS or Pteridophytes and Phanerogams. A separation of the tissues into the three systems of epidermal, fundamental, and vascular tissue occurs for the first time in the vascular plants associated with the development of roots; while the systems themselves also exhibit a widely extended division of labour.

The Ontogeny of the Internal Structure

Just as the phylogenetic development of the vegetable kingdom has proceeded from the simple to the complex, every plant in its ontogeny passes through a corresponding development. The study of the ontogenetic development is termed embryology. The early stage of a new plant body is called the embryo or germ, and its further development is spoken of as germination.

However a plant may arise, whether from an asexually produced spore or from a fertilised egg, its first inception is always as a single cell. In unicellular, spherical, or rod-shaped organisms, such as *Gloeocapsa polydermatica* (Fig. 1) or Bacteria (Fig. 4), the whole course of development is concluded with the cell division which gives birth to two new independent organisms (Fig. 1). If the cell divisions be continuous and parallel, and the newly developed cells remain in contact, CELL FILAMENTS (Fig. 4 *a**) will be formed; if the division walls have different inclinations, and are at the same time all in the same plane, CELL SURFACES are produced; and if the walls are formed in three dimensions of space, CELL MASSES are the result. Such an organism will attain but a low degree of development if all its cells have a like value. With the distinction into BASE and APEX a plant manifests a higher degree of differentiation. A VEGETATIVE or GROWING POINT is then developed, usually at the apex (Fig. 5). This retains its embryonic nature, while the parts produced from it attain a mature condition, a distinguishing feature of the ontogeny of plants as compared with animals (p. 4). In more simply constructed plants the growing point consists of a single cell. This assumes more and more the character of an APICAL CELL from which all the organs of the plant take their origin; thus, in the case of *Cladostephus verticillatus* (Fig. 7), the many-celled main axis terminates in a single conical cell which, by transverse and longitudinal divisions, gives rise to the cellular system of the whole plant. Its lateral branches are likewise formed from similar apical cells, which develop, in regular acropetal order, from certain of the lateral cells of the parent stem, and determine the character of the branching. Flat, ribbon-like plants also, such as *Dictyota dichotoma* (146) (Fig. 8), may have conical but correspondingly compressed apical cells (Fig. 162 *A*), from which segments are cut off by concave cross walls, and become further divided by subsequent longitudinal walls. The dichotomous branching so apparent in *Dictyota* is preceded by a longitudinal division of the apical cell into two equal adjoining cells (*B*, *a*, *a*). By the enlargement and continuous division of these two new apical cells the now bifurcated stem becomes prolonged into two forked branches. In other ribbon-like Algae, on the other hand, and in similarly shaped Hepaticae, as in *Metzgeria* and *Aneura* (147), the apical cell is wedge-shaped (Fig. 163), and the successive segments are cut off alternately right and left by intersecting oblique walls; from these segments the whole body of the plant is derived by further division. The apparently strictly dichotomous branching of Hepaticae

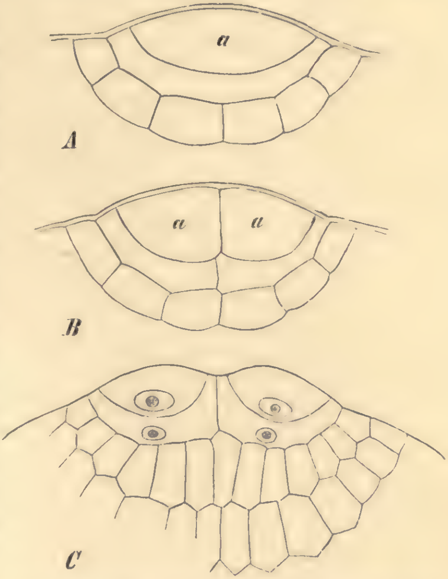


FIG. 162.—The growing point of *Dictyota dichotoma*, showing the dichotomous branching. *A*, Initial cell. (After E. DE WILDEMAN, × 500.)

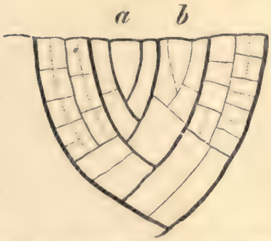


FIG. 163.—Diagrammatic representation of the apex of *Metzgeria furcata* in process of branching, viewed from the dorsal side. *a*, Apical cell of parent shoot; *b*, apical cell of daughter shoot. (After KNY, × circa 370.)

provided with such apical cells is in reality due to the early development of new apical cells in young segments (Fig. 163 *b*). In the case of the erect radially symmetrical stems of the Musci, most Ferns and Equisetaceae, the apical cell has generally the shape of an inverted three-sided pyramid ([148]) with a convex base, and forms the apex of the vegetative cone characteristic of the more highly organised plants. In the common Horse-tail (*Equisetum arvense*), for example, the apical cell of the main axis viewed from above (Fig. 165 *A*), appears as an equilateral triangle, in which new walls are successively formed in a spiral direction, parallel to the original walls (*p*). Each new segment thus derived is divided by a new division wall (Figs. 164, 165 *m*) into an upper and lower half; each of these halves, as is shown most clearly by an optical section just below the apical cell (Fig. 165 *B*), becomes again divided by a sextant wall (*s*) into two new cells. It is unnecessary to trace the further divisions, and it will suffice to call attention to the fact, that all cell walls parallel to the outer surface of such vegetative cones or portions of plants are termed PERICLINAL WALLS, while such as meet the surface and the periclinal walls at right angles are designated ANTICLINAL; of the latter those in the plane of the axis of an organ are called RADIAL. Some distance below the apical cell of *Equisetum arvense* the first leaf-whorl arises from the vegetative cone as a circular ridge, which grows by

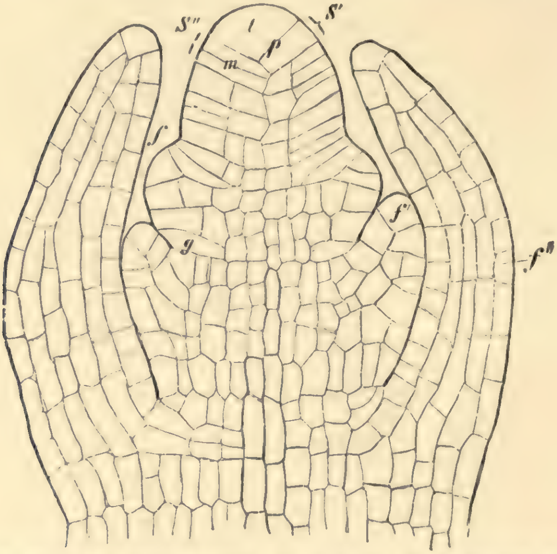


FIG. 164.—Median longitudinal section of the vegetative cone of *Equisetum arvense*. Explanation in the text. (× 240.)

the formation of cell walls inclined alternately inwards and outwards in the wedge-shaped marginal cells (Fig. 164 *f*). This is succeeded at a lower level by other and older leaf-whorls (*f′*, *f″*). An initial cell (*g*) may be distinguished in the axil of the second leaf-whorl, and this is destined to become the three-sided apical cell of a side branch.

In the Lycopodinae, the most highly developed of the Pteridophytes, a distinct apical cell can no longer be recognised, while in the Phanerogams the cells of the vegetative cone are arranged as shown in the accompanying figure of *Hippuris vulgaris* (Fig. 166), in which the embryonic tissues are arranged in layers which, as was first noticed by SACHS (149), form confocal parabolas. The outermost layer, which covers both the vegetative cone and also the developing leaves, is distinguished as the DERMATOGEN (150) (*d*); the cells of the innermost cone of tissue, in which the central cylinder terminates, constitute the PLEROME (*pl*); while the layers of cells lying between the dermatogen and plerome are called the PERIBLEM (*pr*). In the same figure may be noticed the uniformity with which the dividing walls of the different layers intersect at right angles. This arrangement was regarded by SACHS as characteristic of the whole plant structure. The anticlinal walls at right angles to the surface form a system of orthogonal trajectories with the periclinal walls.

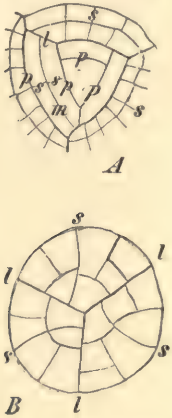


FIG. 165.—*A*, Apical view of the vegetative cone of *Equisetum arvense*; *B*, optical section of the same, just below the apical cell; *l*, lateral walls of the segments. (× 240.)

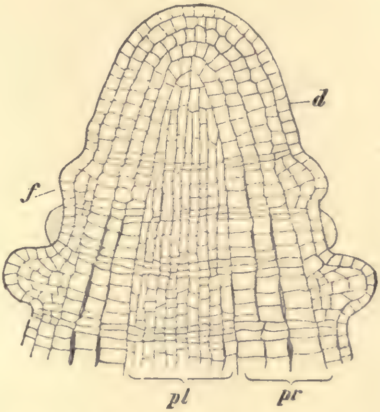


FIG. 166.—Median longitudinal section of the vegetative cone of *Hippuris vulgaris*. *d*, dermatogen; *pr*, periblem; *pl*, plerome; *f*, leaf rudiment. (× 240.)

While SACHS regarded the insertion of new cell walls at right angles to pre-existing ones as the principle of their succession, BERTHOLD and ERRERA (151) have endeavoured to show that the curvature and mode of insertion of a partition wall obey the same laws as do weightless films of liquid. The cell wall tends at the moment of its origin to assume the same position as a film in a mass of soap-suds would under similar conditions.

True ROOTS are first found in the Pteridophytes, and in them possess an apical cell in the shape of a three-sided pyramid (152) (Fig. 167 *t*). In addition to the segments given off by the apical cell parallel to its sides, it also gives rise to other segments (*k*) parallel to its base. It is from the further division of these latter cap-like segments that the ROOT-CAP is derived. In those ferns in which the root may form a terminal shoot (p. 47) the apical cell of the root according to the investigations of ROSTOWZEW (153) forms the apical cell of the new shoot. It ceases to give off segments parallel to the base, and the segments divide differently from those forming the root. In the roots, as in the stems of the Lycopodinae, no apical cells are found. In like manner the roots of Phanerogams, although exhibiting several different types of apical growth, follow the same law in the arrangement of their elements as the vegetative cones of

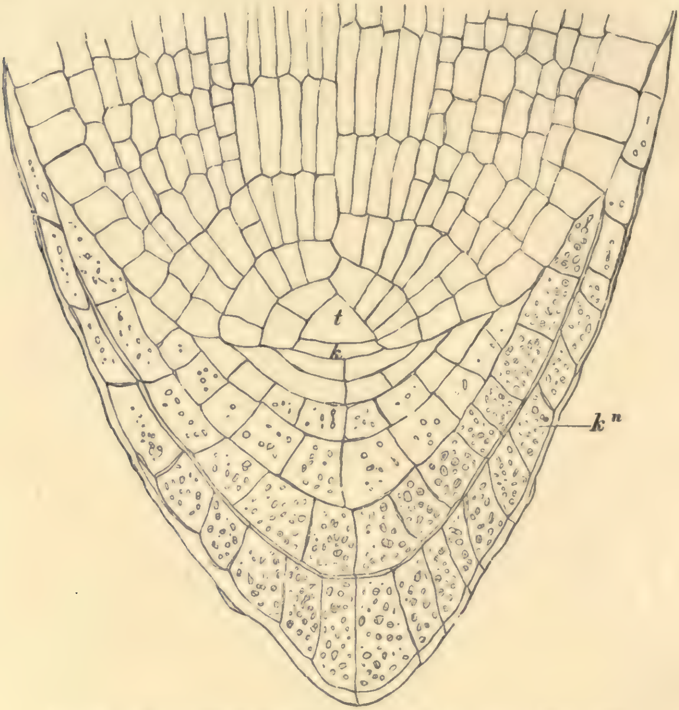


Fig. 167.—Median longitudinal section of the apex of a root of *Pteris cretica*. *t*, Apical cell : *k*, initial cell of root-cap ; k^n, root-cap. (× 240.)

the stems. It will, accordingly, be sufficient to describe a root of one of the Gramineae (Fig. 168) as a representative of one of these types (154). The vegetative cone of this root differs from that of the stem previously described (Fig. 166) in the possession of a root-cap.

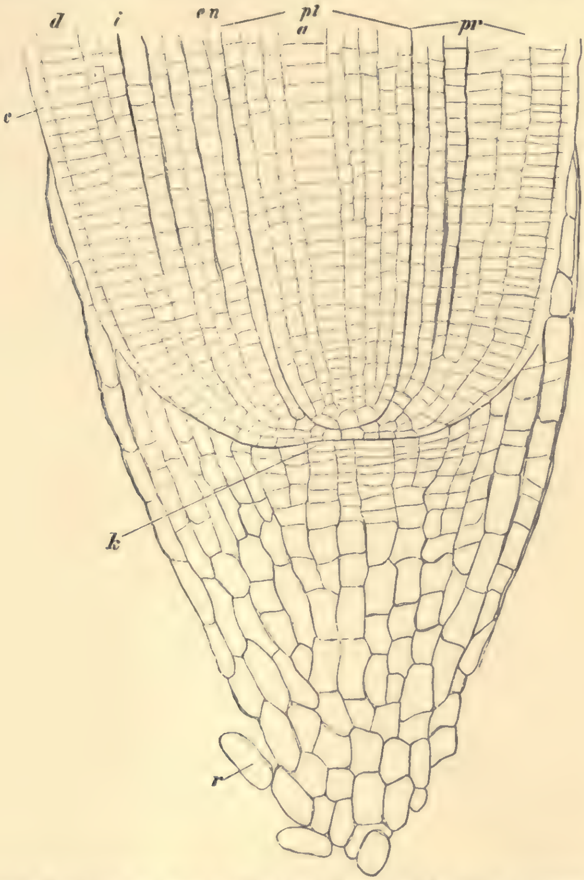


FIG. 168.—Median longitudinal section of the apex of a root of the Barley, *Hordeum vulgare*. *k*, calyptrogen ; *d*, dermatogen ; *e*, its thickened wall ; *pr*, periblem ; *pl*, plerome ; *en*, endodermis ; *i*, intercellular air-space in process of formation ; *a*, cell row destined to form a vessel ; *r*, exfoliated cells of the root-cap. (× 180.)

The dermatogen (*d*) and periblem (*pr*) unite at the apex in a single cell layer, outside of which lies the CALYPTROGEN (*k*) or layer of cells from which the root-cap takes its origin. In many other roots, however, the formation of the root-cap results from the periclinal division of the dermatogen itself, which, in that case, remains distinct from the periblem. In the apices of Gymnosperms the dermatogen, periblem, and calyptrogen are not marked out as distinct regions. In roots, as in stems, the plerome cylinder (*pl*) almost always terminates in special initial cells.

At a short distance below the growing point the embryonic tissue loses its meristematic character, and becomes transformed into the differentiated body of the plant. As a general rule, in plants with an epidermis, primary cortex, and central cylinder, the epidermis is developed from the dermatogen; the primary cortex from the periblem; the central cylinder from the plerome. This differentiation of the tissues does not take place in all cases; an already determined separation of the several tissues must not be assumed to extend to the embryonic tissue, the peculiar cell arrangement of which is due rather to physical causes. The vascular bundles must pass through the periblem in order to reach the leaves. The periblem is therefore capable of producing, not only the primary cortex, but also the vascular bundles and accompanying tissues of the central cylinder. The terms dermatogen, periblem, and plerome are employed merely for convenience to designate certain cell layers, and are not to be regarded as significant of any peculiar histogenetic or tissue-forming ability. The external layer from which the epidermis develops usually remains a single cell layer. The rudiments of the still undeveloped vascular bundles soon appear in the central cylinder as procambium strands; while the endodermis of roots is derived at an early stage from the innermost layer of the cortex.

In stems with apical cells the RUDIMENTS OF NEW LEAVES and SHOOTS are developed from single peripheral cells, or cell groups of the vegetative cone (Fig. 164). In such cases, not only the new shoots, but even the leaves, usually begin their development with an apical cell. The apical cells of the leaves, however, soon disappear, and further growth proceeds along their whole margin.

In those fern leaves which are able to form terminal buds (p. 31) GOEBEL (155) has observed the direct transition of the two-sided apical cell of the leaf tip to the three-sided pyramidal apical cell of the young shoot; this takes place by the origin of a suitably placed wall in the apical cell of the leaf.

In a stem with no apical cell (Figs. 17, 166), the rudiments of the leaves and new shoots first appear as small protuberances, the formation of which is generally initiated by the periclinal division of a group of periblem cells; while the cells of the overlying dermatogen continue to divide by walls at right angles to the surface. In the case of new shoots developing at some distance from the growing point of the parent stem, the cells from which they are destined to arise retain for that purpose their original embryonic character. The formation of the buds on the rapidly growing shoots of bushes and trees in the spring may be postponed, so that the rudimentary lateral shoots first appear in the axils of the eighth or even the tenth youngest leaves, and consequently at points where the differentiation of the surrounding tissue has already begun (156).

The vegetative cone, in the case of strictly dichotomously branching shoots (cf. p. 19), increases the number of its cells in the direction of the plane of the subsequent bifurcation, and eventually gives rise to two new growing points.

With the exception of those Pteridophytes whose roots as well as stems are dichotomously branched (cf. p. 46), the branches of all other normal roots, whether growing by means of an apical cell or not, arise in acropetal succession; the branching first begins in regions considerably removed from the growing point, where the differentiation of the tissues is already complete. In Phanerogams new roots are developed in the pericycle: in Pteridophytes in the innermost cortical layer. The lateral roots must consequently push through the whole cortical layer of the parent root. They are situated either directly opposite to the vascular strands of the parent root, or between the xylem and phloem strands. The number of rows of lateral roots is, therefore, as VAN TIEGHEM (157) pointed out, either equal to or double the number of vascular strands. As the strands of the vascular bundles of roots take a straight course, the lateral roots must similarly form straight rows. The distances between the rows themselves are either equal, or, when the lateral roots are situated to the right and left of each vascular strand, the rows are arranged in pairs with wider intervals between each pair.

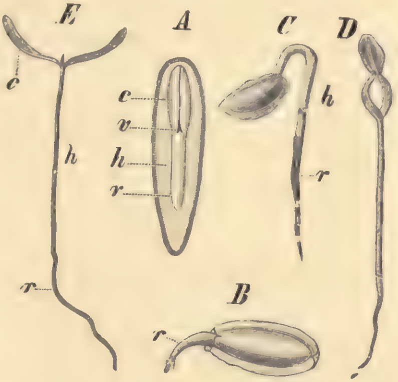


FIG. 169.—*Thuja occidentalis*. *A*, Median longitudinal section through the ripe seed (× 5). *B*, *C* (× 2); *D*, *E* (nat. size), different stages of germination; *h*, hypocotyl; *c*, cotyledons; *r*, radicle; *v*, vegetative cone of stem.

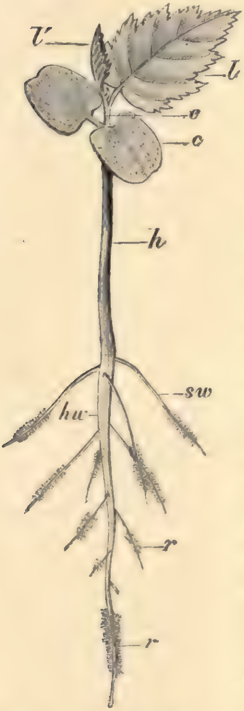


FIG. 170.—Seedling of *Carpinus Betulus*. *h*, Hypocotyl; *c*, cotyledons; *hw*, main root; *sw*, lateral roots; *r*, root-hairs; *e*, epicotyl; *l*, *l'*, foliage leaves. (Nat. size.)

The stage of the ontogeny of the plant known as GERMINATION is specially defined in Phanerogams, where the term is limited to the further growth of the embryo already present within the seed. The embryo, enclosed within the seed, by the time the latter is shed from the parent plant generally exhibits the segmentation characteristic of Cormophytes. Protected by the hard seed-coats, it is enabled to sustain a long period of rest. Abundant deposits of nutritive material in the embryo itself, or surrounding it, are provided for its nourishment during germination. The different segments of a phanerogamic embryo have received distinctive names; thus, as in the embryo of the American Arbor Vitae (*Thuja occidentalis*, Fig. 169), the stem portion (*h*) is termed the HYPOCOTYL, the first leaves (*c*) are the **SEED LEAVES** or COTYLEDONS, while the root (*r*) is distinguished as the RADICLE. The tap-root of the fully-developed plant is formed by the prolongation of the radicle and later gives rise to lateral roots. In Fig. 170 a germinating plantlet of the Hornbeam (*Carpinus Betulus*) is shown with its hypocotyl (*h*) and two cotyledons (*c*); its radicle has already developed into a tap-root (*hw*) with a number of lateral roots (*sw*). An internode and foliage leaf (*l*) have been produced from the vegetative cone of the stem; while the next higher internode is also distinguishable, but has not yet elongated, and a second foliage leaf (l^1) is unfolding.

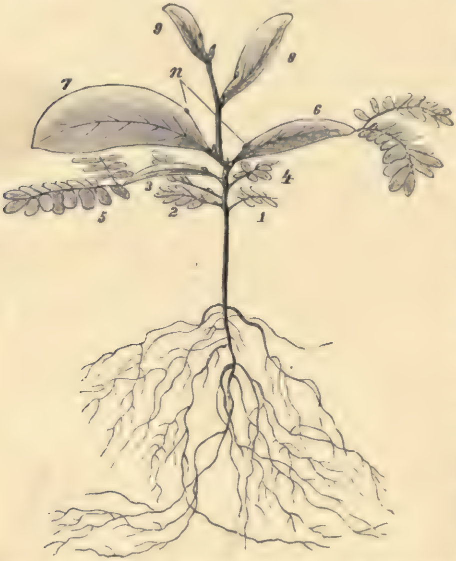


FIG. 171.—Seedling of *Acacia pycnantha*. The cotyledons have been thrown off. The foliage leaves 1-4 are pinnate, the following leaves bipinnate. The petioles of leaves 5 and 6 are vertically expanded; and in the following leaves. 7, 8, 9, modified as phyllodia, bearing nectaries, *n*. (About ½ natural size.)

A highly organised plant, which begins its development with the simplest stages and gradually advances to a higher state of differentiation, to a certain extent repeats in its ontogeny its phylogenetic development. In the process of its ontogenetic development much has been altered, and much omitted, so that it presents but an imperfect picture of its past history; nevertheless, this representation is valuable, and, next to comparative methods, furnishes the most important source of our morphological knowledge. Whatever is true of the development of a plant from the embryo is also, as a rule, applicable to its further growth from the growing point, and, consequently, a knowledge of the mode of development at the growing point is of great importance in establishing homologies. The earlier a characteristic makes itself apparent in the embryo, or the nearer it is to the growing point of the old plant, so much the greater is its value in determining the general relationships existing between the different plants; the later it is exhibited in the embryo, or the farther removed it is from the growing point of the plant, the less its general value, but the greater, in proportion, its importance in defining the character of a genus or species. From the fossil remains of former geological periods, it is safe to conclude that such Conifers as *Thuja*, *Biota*, and the various Junipers, that now have scale-like compressed leaves, have been derived from Conifers with needle-shaped leaves. This conclusion is confirmed by the fact, that on the young plants of the scaly-leaved Conifers typical needle-shaped leaves are at first developed. The modified leaf forms do not make their appearance until the so-called JUVENILE FORM has attained a certain age, while in some Junipers needle-shaped leaves are retained throughout their whole existence ([158]). Even still more instructive are the Australian Acacias, whose leaf-stalks become modified, as phyllodia (p. 45), to perform the functions of the reduced leaf-blades. The demonstration of such an assertion is furnished by a germinating plant of *Acacia pycnantha* (Fig. 171), in which the first leaves are simply pinnate, and the succeeding leaves bipinnate. In the next leaves, although still compound, the leaf-blades are noticeably reduced, while the leaf-stalks have become somewhat expanded in a vertical direction. At length, leaves are produced which possess only broad, flattened leaf-stalks. As many other species of this genus are provided only with bipinnate leaves, it is permissible on such phylogenetic grounds to conclude that the Australian Acacias have lost their leaf-blades in comparatively recent times, and have, in their stead, developed the much more resistant phyllodes as being better adapted to withstand the Australian climate. The appearance, accordingly, of the phyllodes at so late a stage in the ontogenetic development of these Acacias is in conformity with their recent origin. *Lathyrus aphaca* (p. 44) the leaves of which in the mature plant are transformed into tendrils, has the first leaves of the seedling provided with leaflets. It may, in like manner, be shown that in the case of plants with similarly modified leaf forms, the metamorphosis of the leaves does not take place until after the cotyledons and the first foliage leaves have been developed, and it is then usually effected by degrees.

In the lower divisions of the vegetable kingdom, especially among the Fungi, PLEOMORPHISM is a phenomenon of frequent occurrence. In the developmental cycle of the species more than one living being or biont is found, and the bionts are characterised by differences in form. Thus in the Rust of Wheat (*Puccinia graminis*) the individuals which live on the Barberry produce as reproductive organs æcidia and spermogonia. From them arise the quite distinctly organised biont living on the leaves and stems of grasses which is reproduced by means of uredospores and teleutospores. From the latter, on damp soil in the spring, tubular germ-plants arise which in their turn bear a special kind of reproductive cell, the basidiospores. With this type of spore the developmental cycle of the species is completed, since from the basidiospores are again formed the individuals which live on the Barberry.

In treating of the cell processes which constitute fertilisation (p. 92), it has already been seen that they result in a doubling of the number of chromosomes present in the nucleus. Doubtless, the process of fertilisation has repeatedly originated in both animal and vegetable kingdoms as soon as a certain grade of organisation had been attained in the course of phylogenetic development. In every case the process of fertilisation must have resulted in a doubling of the number of chromosomes. The single chromosome number must be assumed to be the number originally occurring in the organism. According to the view of most investigators the chromosomes are persisting entities in the nucleus. Further, there is much in favour of the view that they are different from one another. Under these conditions the doubling of the number of chromosomes in the act of fertilisation would lead to a progressive increase in their number if the reduction division (p. 84) had not been introduced into the course of development of the organism ; in this division the number is reduced to one half, that is to say, a return is made to the original condition. If in the ontogeny of an organism, the reduction division follows immediately on fertilisation all the bionts of the species will show the single number of chromosomes. This was, in any case at first after the distinction of sex, always the condition of things, and it is found in many existing Thallophytes. In the further course of phylogenetic development the sexual product developed into a special biont, which accordingly had the double number of chromosomes in its tissues. Not until the formation of its reproductive cells did this biont proceed to the reduction division by which the number of chromosomes returned to the original single number. When in the developmental cycle of a species bionts with the single chromosome number and others with the double number are represented, we have to do with an alternation of generations. Such an alternation of generations is found in all Bryophyta, Pteridophyta and Phanerogams, *i.e.* in plants from the Bryophytes onwards. The generation with the double number of chromosomes became in these plants the dominant one, while that with the single number underwent a progressive diminution in size. Thus the plant body which is most prominent in Pteridophytes and Phanerogams is the generation with the double number of chromosomes, while the corresponding generation with the single number becomes so inconspicuous that it ultimately requires to be carefully looked for. This is especially the case for the Phanerogams, in which this generation no longer has an independent existence, but completes its development within the generation with the double number of chromosomes. The generation with the single number of chromosomes is in plants termed the gametophyte ; that with the double number the sporophyte. In order to extend the distinction to the animal kingdom the terminology must be altered ; the organism with the single number of chromosomes may be termed the haploid, or haploid generation, that with the double number the diploid, or diploid generation.

The union of paternal and maternal chromosomes in each sexual act results in the nuclei of the offspring being provided with maternal and paternal chromosomes in equal numbers. All the nuclei of a diploid generation contain each kind of chromosome in duplicate in two equivalent chromosomes. In the reduction division by which the formation of the reproductive cells is prepared for, the chromosomes become united (as has been seen on p. 84) in pairs during the prophase of the division. It is to be assumed that the pairs are formed of the corresponding parental chromosomes. In the separation which follows during the metaphase of the reduction division each chromosome may apparently pass to either of the two daughter nuclei, but always in such a manner that the chromosomes of each pair pass to different nuclei. Thus on the one hand, all combinations of the parental chromosomes are possible in the products of this division ; on the other hand a chromosome of each kind is ensured to each of the resulting nuclei. All these morphological processes, which are matters of observation, lend great support to the assumption that the nuclei are the bearers of the inherited properties of the organism (159).

By those apogamous processes which exclude a reduction division (p. 93) an alternation of generations is also abolished.

Structural Deviations (160)

Plants, even of the same species, never exactly resemble each other. Every individual organism has its own peculiar characteristics by which it may be distinguished from every other of the same species. To a certain extent these characters may be due to ATAVISM, or the reappearance of previous ancestral qualities. Most individual deviations belong, however, to the so-called FLUCTUATING VARIATIONS. These occur in all species, and may be compared to the excursions of a pendulum to either side of its position of equilibrium. Abrupt and striking deviations of the individual from the type of the species are called MONSTROSITIES. When these induce a disturbance of function a diseased condition results. The causes of monstrosities may lie in the organism itself ; in other cases they can be shown to stand in relation to external causes. Among EXTERNAL CAUSES OF VARIATIONS the influence exercised by parasites upon the development of the portions of the plant is particularly striking. *Euphorbia Cyparissias*, when attacked by a rust fungus (*Aecidium Euphorbiae*), becomes sterile, remains unbranched, has shorter and broader leaves, and in its whole appearance is so changed as scarcely to be recognisable. Plant lice sometimes cause a flower to turn green, so that instead of floral leaves green foliage-like leaves appear. Another peculiar example of abnormal growths is afforded by the GALLS or CECIDIA produced on plants by Fungi, or more frequently by insects, worms, and arthropods. The effect of these formations on the normal development of the tissues of a plant is more or less disturbing, according to their position, whether it be in the embryonic substance of the growing point, in the tissues still in course of differentiation, or finally in those already developed. The larvæ of *Cecidomyia rosaria* live in the growing points of Willow stems, and occasion a malformation of the whole shoot by the production of galls, known as "willow-roses," which are composed of modified leaves and axes. Flies (Diptera) often deposit their eggs in the tissues of partially developed leaves, in consequence of which the leaves become, according to their age when attacked, more or less swollen and twisted. After the leaves of the Oak have attained their full growth they are often stung by a gall-wasp of the genus Cynips. The poison introduced by the sting, and also by the larvæ hatched from the eggs deposited at the same time, occasions at first only a local swelling of the leaf tissue, which, finally, however, results in the formation of round, yellow, or red galls on the lateral ribs on the under side of the leaf. As galls differ materially from one another according to the nature and cause of their formation, it is generally possible to determine the particular exciting cause to which they are due.

In the monstrosities resulting from internal causes it is also the case that the earlier they commence the more extreme they tend to be. When the embryonic substance of the growing point is affected by such an influence altogether unexpected modifications of the usual order of growth may result. In other cases intermediate structures of more or less monstrous form result. As the embryonic substance of the growing point is of itself capable of producing all such forms as are peculiar to the species, instead of a flower a vegetative shoot may be developed, or the growing point of a root may continue its further development as a stem. Leaves, even when somewhat advanced in growth, may under changed conditions vary their usual character, particularly within the limits of their possible metamorphosis; for example, the staminal and carpellary leaves of a flower may thus become transformed into additional perianth leaves. The later the rudiments of an organ are acted upon by a disturbing influence, so much the less far-reaching are the modifications which are produced; thus intermediate forms between two organs may be produced which correspond more or less closely to one or the other of them. Neither the abnormal interchangeability, at times manifested between morphologically different members, nor the development of intermediate forms between them, can be considered as proof of their phylogenetic connection. MALFORMATIONS ARE, ACCORDINGLY, TO BE ACCEPTED AS EVIDENCE IN MORPHOLOGICAL QUESTIONS ONLY IN THE RAREST CASES. When, as is only exceptionally the case, they represent reversions, this value may be attached to them.

The study of the abnormal formations and functions of the plant is called PHYTOPATHOLOGY. When the pathological structures are alone in question it may be termed pathological morphology. Malformations which affect the external form are still treated by themselves as Vegetable Teratology (Phytoteratology). Pathological changes in the form and contents of the vegetable cells and tissues form the subject matter of pathological plant anatomy.

The study of the ætiology of abnormal vegetable tissues shows that various external influences may give rise to them; the most important causes are the influence of wounding and of the attacks of parasites. According to ERNST KÜSTER abnormal cells may be characterised by their contents, the thickening of their walls, or by their unusual size (hypertrophy); in the last case they may also show divisions which would not normally occur. The abnormal tissue may resemble that from which it originates or deviate more or less widely from it. The tissues formed in the healing of wounds (cf. p. 151) and those of galls may be mentioned as examples. The tissues of galls are characterised more by the increase in number than by the size of their cells, which may undergo the most various modifications. There is often a considerable accumulation of albuminous substances and carbohydrates in these tissues. A modified part of a plant in many cases appears as if due to an arrested development. Dwarf forms and defective differentiation of tissues with its accompanying impairment of function are examples of this. In all cases in which the cells of a tissue no longer present their normal properties they are liable to undergo sooner or later regressive changes leading to degeneration and necrosis.

PART I

GENERAL BOTANY

SECTION II

PHYSIOLOGY

SECTION II

PHYSIOLOGY

PLANTS, like animals, are living organisms. Beginning their development with the simplest structure, and increasing in size from internal causes, they assume their definite form and complete their existence according to laws determined by inheritance. Surrounded by a world, which differs very widely from them as regards chemical constitution, they produce the substances necessary to their growth from the raw materials afforded by the environment. To this end the different parts of their bodies are enabled by independent movements to take such relative positions as are most favourable to their mode of growth. Like other living beings plants sooner or later perish. In spite, however, of the limited duration of life and number of individuals, the continuance and extension of the species are provided for by an ability to reproduce like organisms.

NOURISHMENT, INDEPENDENT GROWTH, POWER OF MOVEMENT, and REPRODUCTION are, together with RESPIRATION, the most striking attributes which characterise plants as living organisms, and distinguish them from all lifeless bodies.

An organism consisting of but one cell, as is shown by the life of the simplest plants, is capable of exercising all the functions necessary for the continuance of its existence. In the case of plants, however, which consist of many hundreds or thousands of cells arranged in three dimensions of space, it is impossible, for purely physical reasons, that all the cells should bear the same relations to the outer world. The cells in the interior must exist under conditions altogether different from those which are in direct contact and intercourse with the world outside. Consequently, the differently arranged elements must be adapted for different modes of life, and, since they exercise their functions in different ways, they show what is called DIFFERENTIATION.

This necessary division of labour has led to the development of external organs and internal structures wonderfully adapted to the requirements of the whole plant. Correlated with the natural groups of plants, there are certain differences as regards form and function. In all plants, however, those organs to which the same functions are assigned have assumed the form most efficient for their purpose; so that, for example, the leaves and roots of plants otherwise most dissimilar are constructed on the same general plan. In proof of this may be cited the general terms leaf, root, stem, and flower, the comprehensiveness of which is even more evident in popular speech than in the technical language of Botany, which has given to these terms a more strictly defined and limited meaning.

Similarity in the appearance and structure of organs indicates the exercise of common functions and duties; while dissimilarities in the form and structure of different organs—such as the leaf and root—are indicative, on the other hand, of their different utility to the plant. There lies, then, in the morphological and anatomical development of an organ an unmistakable proof that it exists because of its function, and that it is not of accidental origin.

The attributes and functions of organs, as well as of single cells, are the subjects of physiological study. It is evident, however, that such study must be based upon an intimate knowledge of the outer and inner structure of plants; just as the working and efficiency of a machine first become comprehensible through a knowledge of its construction. The principal and most reliable source of physiological knowledge is, however, obtained by experiment.

It is the province of Physiology to discover the points of correspondence among the numerous individual phenomena, and to bring to light such as possess an essential functional significance. On the other hand, it is the variations, or family peculiarities, which are of value in Systematic Botany, since from them a knowledge of family relationships may be derived. For example, it suffices for the physiological understanding of flowers to know that they are the organs of sexual production in higher plants; that the male cells are somehow developed from the pollen formed in the anthers; that from the female cell enclosed within the ovules, after its union with a male cell from the pollen-tube the embryo or rudimentary plant is derived. These important facts are equally true for all flowers, no matter how dissimilar they may appear.

Physiology considers peculiarities of form in so far as they are of service for special purposes arising from the relation of the plant to its surroundings (Pollination, Distribution of Seeds, Water-plants, etc.). This side of physiology is termed BIOLOGY, or better ŒCOLOGY (Bionomics) since the former term is often applied to the science of living beings in general.

The Physical and General Conditions of Life and Vital Properties of Plants

With the exception of the more or less fluid developmental stages in some of the lower organisms, as in *Amœba* or the plasmodia of

Myxomycetes (p. 54), plants, in spite of the great amount of water contained in them, are of the nature of solid bodies. As such they possess in common with inanimate objects the physical attributes of weight, rigidity, elasticity, conductivity for light, heat, electricity, etc. Important as these attributes are for the existence and continuance of the life of a plant, they do not constitute that life itself.

VITAL PHENOMENA ARE ESSENTIALLY BOUND UP WITH THE LIVING PROTOPLASM. No other substance exhibits a similar series of remarkable and varied phenomena, such as we may compare with the attributes of life. As both physics and chemistry have been restricted to the investigation of lifeless bodies, any attempt to explain vital phenomena solely by chemical and physical laws could only be induced by a false conception of their real significance, and must lead to fruitless results. The physical attributes of air, water, and of the glasses and metals made use of in physical apparatus, can never explain qualities like nutrition, respiration, growth, irritability and reproduction. It would, indeed, be superfluous to emphasise the fact, were it not that this error is from time to time repeated.

The phenomena of life can only be studied and determined by the most careful observation and critical examination of living organisms. It is therefore necessary to establish what part the purely physical and chemical properties which belong to all bodies, take in the phenomena of life, and to what extent they are essential to the maintenance of life itself. A perception of the strictly physical and chemical processes going on within an organism is especially desirable, though their exact determination is not more important than that of the vital reactions, because operations are then involved with the causes and effects of which we are already familiar. In questions regarding strictly vital phenomena the case is quite different; for it then becomes impossible to predict what effect a particular cause will produce.

The free end of a horizontally extended flexible rod bends downwards merely by its own weight. The same result will follow if any part of a dead plant, such as a dry stem, be substituted for the rod. But if a living, growing stem be used in the experiment, then the action of gravity will manifest itself in a manner altogether at variance with its ordinary operation. That part of the stem which is still in a state of growth will ultimately curve upwards, and BY ITS OWN ACTIVITY ASSUME AN UPRIGHT POSITION; it moves in a direction exactly contrary to the attractive force of gravity. If a tap-root be similarly experimented upon, it will, on the contrary, continue its downward movement until it places itself in a line with the direction of the attraction; a rhizome, however, under like circumstances, would constantly maintain its growing apex in a horizontal position. In these three experiments the force of gravity is exerted upon horizontal portions of plants. The physical conditions are the same in each case, yet how entirely different the results!

The explanation of this dissimilarity in the effects of the action of gravity is to be sought in the fact that gravity acts upon living substances, not only physically but also in another way, as a stimulus which induces a response in the internal activities of the plant body. In these particular experiments it is the processes and forces of growth which are locally increased or hindered by the action of gravity, and produce results which do not correspond either qualitatively or quantitatively with the known operations of the laws of gravity. Living substance is dominated by the operation of stimuli. Irritability is its most important attribute, for it is irritability alone that renders possible what we call life.

By irritability is meant the undoubted, though not fully understood, causal connection between a particular influence and the peculiar vital response of an organism. The disproportion that may exist between an influence and its ultimate effect is plainly apparent in a steam engine or in the firing of firearms. The slight pressure of the finger in firing a cannon has as little correspondence, either quantitatively or qualitatively, with the destructive effect of the shot, as the small effort necessary to open the throttle-valve of a locomotive has to the continuous motion of a heavily laden goods train. The opening of the valve of an engine before the steam is up has no effect; it is only when, by this process, the compressed steam is liberated that it is followed by such enormous results. In the engine the connection between the external influence and its effect is known; in the effects of stimuli on protoplasm this connection is not apparent, for in the protoplasm the intermediate processes remain invisible to the eye, even when aided by the best microscope. There is, however, no occasion for the supposition that the connection between the stimulating cause and its effect on the protoplasm is accomplished by processes which are otherwise foreign to the protoplasm itself, and which are called into existence only under the influence of a special force, the vital force. It was formerly thought necessary to ascribe not only all indications of life, but even all the transforming processes carried on within animate objects, to the effects of a special vital force. Now, however, the conception of the vital processes has become so modified as no longer to require the supposition of such a special vital force; while the impossibility of explaining the manifold variety of their manifestation by the action of a single force, and the advances made in chemistry (cf. pp. 4, 5), have shown the futility of such a supposition.

Although, at the present time, the existence of a special, independent vital force is denied by Physiology, and only such agencies are accepted as are inherent in the substance of an organism itself, still we must at the same time take account of such a vital force in so far as it may be regarded as the expression of a living substance, endowed with a peculiar, internal structure, which is in some way so constituted that certain actions and conditions are followed by definite vital processes. It is, then, this peculiar quality of irritability that distinguishes living protoplasm from other bodies, and constitutes the fundamental distinction between living and dead protoplasm. Such a view is, however, not contrary to accepted ideas; simple chemical bodies, indeed even chemical elements, such as sulphur, phosphorus, etc., exist in different "modifications" with fundamentally different peculiarities. In considering living organisms, it is the irritable or living modification of the protoplasmic substance which must occupy the attention. The object, therefore, of Physiology consists principally in discovering the attributes and characteristics incident to the modifications of living protoplasm.

These attributes and characteristics are so distinctive as to separate by a wide gap living bodies from all other matter. It is, in fact, impossible to form any conception of the manner in which living bodies have arisen on this once molten planet from lifeless matter. Acceptance of the theory of evolution authorises, it is true, the transfer of the inception of life on the earth to geological periods separated by millions of years from the present time; but the character and condition of origin of such dawning life remain no less incomprehensible. From a consideration, however, of the attributes of the living substance, it can with safety be said that the external conditions of life could not at that time have been so very different from those now existing on the earth; for it is a characteristic quality of living matter that its vital activity, even its very existence, is circumscribed and limited by external, cosmic influences. The vitality of vegetable protoplasm can only be preserved within a definite range of temperature, while its full vital activity is restricted to still narrower limits. Too intense light or too little warmth destroys its life; while the most minute quantities of certain poisons suffice to shatter instantly and irrevocably that mysterious structure, in which, under favourable conditions, lies concealed the capacity to populate the whole world.

Although living plants are themselves responsible for the manner in which their vital phenomena manifest themselves, they stand, nevertheless, in the closest reciprocal relations with their environment, upon the condition of which they are dependent. From the outer world they obtain not only their nourishment, but receive also from it, particularly from the vibrations of light and heat, the energy that they again expend in the manifold processes of their vital phenomena. It is to the operation of these external influences that the stimuli are due, which constantly call forth in vegetable protoplasm the manifestation of vital phenomena. These external influences, however, are only serviceable to the processes of life when they operate within definite limits of intensity. The lowest limit of intensity for the effective operation of an external influence is designated the MINIMUM, the highest the MAXIMUM, while that degree of intensity at which it is operative in calling forth the most active manifestation of a definite vital phenomenon is termed the OPTIMUM. Minimum, optimum, and maximum are not, however, points of fixed value for the organism, but vary, on the one hand, with the duration of exposure; on the other, with the sum of the other conditions. For the different vital processes of the same plant, and also for those of distinct plants, these so-called CARDINAL POINTS are generally different.

The cardinal points for the vegetation of cold climates are on the average much lower than those of plants inhabiting temperate or tropical countries. The distribution of plants over the surface of the earth is thus to a considerable extent dependent on their cardinal points. The highest are not, however, possessed by tropical plants, but by small Algae and Bacteria which inhabit hot springs, the water of which has a temperature of 70°-80° C. The albumen of a hen's egg is quickly coagulated by the water in which these plants find their suitable habitat, while some thermogenic Bacteria can raise their own temperature to 70° C., and even higher.

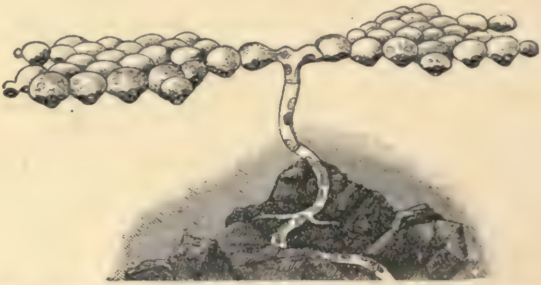


FIG. 172.—Protonema of *Schistostega osmundacea*. The lens-shaped cells concentrate the feeble light available in the habitat of the plant upon the chloroplasts. (Cf. Fig. 214.)

Some plants flourish best when exposed to bright sunlight, while the shade-loving plants only attain their perfect development in a subdued light, such as that of a forest, or like *Schistostega* in crevices and caves (Fig. 172). Not only does the intensity of the required illumination differ for different species of plants, and also for individuals of the same species, but the optimum intensity may change as the development of the individual plant proceeds. Shade is absolutely essential for many tropical plants in a young state, although at a later age they can endure and may even require the full light of the tropical sun. Young plants require to be protected by specially planted shade-producing trees (*Albizzia moluccana*, *A. stipitata*, etc.).

On exposure to a low temperature, about the freezing-point of water, many plants become frozen and generally die. Very sensitive plants may even become frozen at a temperature considerably above zero, before ice has been formed in their tissues. In the case of other plants the internal formation of ice in the tissues does not of itself occasion death. The formation of ice always begins in the intercellular spaces and not within the cells. Its continued formation is accompanied by an increasing concentration of the cell sap; as a consequence of this, ice first begins to form in plants at a temperature below zero, and only gradually increases in case of a greater reduction of temperature (according to MEZ, to −6°). Such plants as inhabit Arctic and Alpine regions are able to recover from the completely frozen condition. The power which the lower organisms have of withstanding extremely low temperatures is very striking. In PICTET's investigations Diatomaceae were found to sustain a long exposure to a temperature of −200° C.; MACFADYEN and others have shown that many Bacteria can endure a week's exposure to 250° of cold produced by means of liquid air and hydrogen (¹).

A sudden change of temperature leading to the complete thawing of frozen plants is better borne than repeated transitions from freezing to thaw. A long, keen frost is therefore, as a rule, less injurious to vegetation than less severe frost alternating with frequent partial thaws.

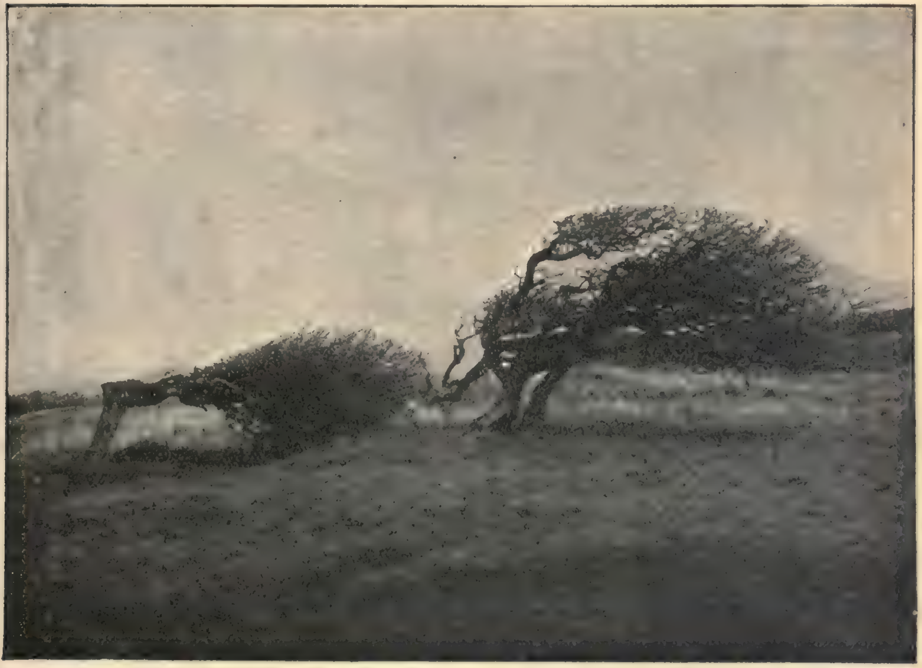


FIG. 173.—Trees on the coast of Denmark; to the left *Prunus spinosa*, to the right *Crataegus oxycantha*, the form of both being similarly modified by the influence of the sea wind. (After WARMING: from SCHIMPER's *Plant-Geography*.)

When the vital powers of reaction of the plant are opposed to purely physical influences, it will naturally depend on their respective strengths which shall become the dominating influence. A centrifugal force a thousand times greater than that of gravity is powerless to influence the reaction of the plant. The degree to which constant and strong currents of air, such as sea-winds, may completely alter the characteristic growth-forms of trees (²) is illustrated by Fig. 173.

I. The Stability of the Plant Body

One of the most important and essential physical attributes of a plant is its rigidity. Without that quality plants could retain no enduring form. Plants which reach a considerable height and by branching expand freely in the air are specially dependent on the rigidity of their bodies so as to remain fixed in the position they have attained. The capacity to return, by their own independent movement, to favourable positions from which they may have been forcibly displaced by external influences, is, in trees and shrubs, and also in the more rigid herbs, restricted to the extreme tips of the growing branches.

How great are the demands made upon the stability of plants will be at once apparent from a consideration of a Rye haulm; although it is composed of hundreds of thousands of small chambers or cells, and has a height of 1500 mm., it is at its base scarcely 3 mm. in diameter. The thin stems of reeds reach a height of 3000 mm. with a base of only 15 mm. diameter. The height of the reed exceeds by two hundred times, and that of the rye haulm by five hundred times, the diameter of the base. In addition, moreover, to the great disproportion between the height and diameter of plants, they often support a heavy weight at the summit; the Rye straw must sustain the burden of its ears of grain, the slender Palm the heavy and wind-swayed leaves (which in *Lodoicea seychellarum* have a length of 7 m. and a breadth of 3-4 m.), while at times the considerable weight of the bunches of fruit has also to be considered.

In plants, however, the rigid immobility of a building is not required, and they possess instead a wonderful degree of ELASTICITY. The rye straw bends before the wind, but only to return to its original position when the force of the wind has been expended. The mechanical equipment of plant bodies is peculiar to themselves, but perfectly adapted to their needs. The firm but at the same time elastic material which plants produce, is put to the most varied uses by mankind; the wood forms an easily worked yet sufficiently durable building material, and the bast fibres are used in the manufacture of thread and cordage.

In young stems and plants, in which the stiff but elastic wood and sclerenchymatous fibres are not developed, the necessary rigidity cannot be attained in the same way as in the older and woody stems. But although the principal component of such young stems is water (often 90 per cent or more), they maintain a remarkable degree of rigidity and elasticity through the elastic tension of their extremely thin and delicate cell walls.

Turgidity.—When air or water is forced, under pressure, into an elastic receptable such as a rubber tube, the walls of the tube become stretched and the tube longer and thicker. By this process the tube becomes just so much stiffer and firmer the greater the internal pressure and the more elastic and thinner its wall. By the similar tension of their elastic cell walls arising from internal pressure, the rigidity and elasticity of thin-walled plant cells, and organs composed of them, are maintained. The internal pressure results from the osmotic attraction and interchanges between the substances dissolved in the cell sap and the water outside the cell.

When two substances in solution are separated by a membrane which is permeable to both, a mixture of the two solutions will take place through the dividing wall. If, however, the membrane is more easily permeated by one of the solutions than by the other, then a larger quantity of the one than the other will pass through it. If the membrane is semipermeable, *i.e.* is only permeable for one solution, that one alone will be drawn through it. If a pig's bladder be filled with a solution of common salt and then immersed in water, the flow of water into the bladder is more rapid than the outflow of the salt solution, and in consequence, an internal pressure is exerted within the bladder sufficient to expand it to a hard rigid body.

A pressure similar to that arising from the osmotic attraction of the salt solution is produced in plant cells by the substances, particularly organic and inorganic acids, salts, and sugars, held in solution in the cell sap. The living protoplasm of the cell does not allow any of the substances dissolved in the sap to pass out except such as escape through the diffusion taking place between the cells themselves, in the constant translocation and exchange of substances within the plant. As may be directly observed in cells with coloured cell sap, the dissolved substances are held in by the protoplasm. These substances, however, draw in water through the cell walls and the protoplasm, and so set up a pressure within the cells of at least 3·5 atmospheres, and often as great as 5–10 atmospheres. In some instances this pressure may amount to 15, 20, or more atmospheres. In the cambial cells of trees a pressure of 25 atmospheres, and in the "nodes" of grasses, of 40 atmospheres is attained. Thus a tension is created which frequently exceeds that exerted by the steam of the most powerful locomotives. Through the force of such a tension the cell walls become so distended, that cells under the influence of this internal pressure or TURGIDITY become longer and larger than in their unexpanded condition.

When, from any cause, the quantity of water in such a turgescent cell is diminished the internal pressure is naturally decreased, and the cell walls, the distension of which may have amounted to 10-20 per cent, again contract. The cell grows smaller, and, at the same time losing its rigidity and elasticity, becomes soft and flaccid.

This condition occurs from natural causes when a succulent plant loses more water by evaporation than it can replace, and, in consequence, wilts. Such a flaccid plant plainly shows that the rigidity is not maintained by its framework of cell walls, but by the hydrostatic pressure within the cells, for with a more abundant water supply it returns to its original condition.

In addition to loss by evaporation, water can also be withdrawn from cells by the same molecular force which causes the internal or endosmotic pressure. In cases where the cells are surrounded by a solution which exerts an attraction upon water, the turgidity of the cells is proportionally weakened, and may be altogether overcome. On account of the consequent **PLASMOLYSIS**, or the contraction and separation of the protoplasm from the cell walls, occasioned by the withdrawal of water, the tension of the cell walls is decreased, and the cell becomes flaccid and collapses (Fig. 174).

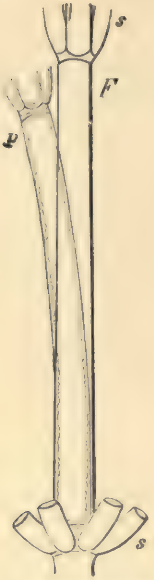


FIG. 174.—Internodal cell of *Nitella*. *F*, Fresh and turgescent; *p*, with turgor reduced, flaccid, shorter and smaller, the protoplasm separated from the cell walls in folds; *ss*, lateral segments. (× circa 6.)

Solutions of non-metallic organic substances possess the same osmotic power when the number of molecules dissolved in the litre is the same; their "equimolecular solutions" are "isosmotic." On account of their dissociation when in solution into ions, metallic compounds exert 1½, 2, 2½ times this osmotic effect. These numbers represent the "isosmotic coefficients" of these substances.

If placed in pure water, however, the previous turgescence of the cells can be restored, if their protoplasm has not been too strongly affected by the action of the solution. If the protoplasm has been killed in the process, it becomes permeable to water, and it is no longer possible to set up an internal pressure. Fresh sections of Beet, placed in water, give up none of their sugar or colouring matter; but after the protoplasm has been killed, the sugar and colouring matter at once escape into the surrounding water, and the sections lose their firmness and rigidity.

On the other hand, Fungi, Bacteria, or marine plants, when placed in a weaker saline solution or in fresh water, have the internal pressure of their cells increased. This may even lead to the rupture of the cell wall (plasmoptysis).

Through a knowledge of the strength of a solution necessary to produce plasmolysis, a means is afforded of measuring the internal pressure within plant cells. For example, if a solution of saltpetre with an osmotic pressure of 5 atmospheres (a 1 per cent solution, according to PFEFFER's investigations, gives rise to a pressure of about 3½ atmospheres) is just sufficient to overcome the turgidity of a plant cell (which in the case of stretched elastic cells shows itself by the limit of contraction being reached), then, conversely, the cell sap exerts upon water an equivalent endosmotic pressure. The force required to forcibly stretch a flaccid or plasmolysed organ to its original length furnishes also a rough means of estimating the pressure developed in turgescent tissues (3).

In the tension produced by turgidity we see how purely physical processes determine the rigidity of plants. These PHYSICAL processes are, however, dependent upon the VITAL functions of plants, inasmuch as they can only be called into action by living protoplasm in conjunction with the structure and properties of the cell. Living plant cells have thus power to regulate the physical effects of osmotic pressure by increasing or diminishing, or even suddenly overcoming their turgidity. (The osmotic pressure is increased three times by the change of glucose into oxalic acid.) It will also be apparent, in considering the operation of other physical forces, that the primary and essential result of the vital action is to give rise to the operation of physical processes, and to favour, constrain, or vary them in such a way that they become of service to plant life.

Tension of Tissues.—The rigidity of parenchymatous tissue, although to a large extent dependent upon the tension arising from the turgidity of its individual cells, is nevertheless considerably enhanced by the opposing pressure between the inner and outer tissue systems, in particular, between the pith and the epidermal and cortical tissues. The pith in this case plays the same part as the cell sap, since it is continually striving to increase its volume; the epidermal and cortical layers, on the other hand, by the pressure of the internal pith cylinders, are stretched and distended, just as are the cell walls by the osmotic pressure of the cell sap.

The tension of tissues is easily demonstrated by removing a strip of the peripheral tissue from a piece of a turgescent stem (of a Sunflower, *Helianthus*, for example), and cutting out the pith. It will be found that the outer tissue at once becomes shorter, and the pith longer than when they were united together in the stem. If the length of the stem experimented upon was 50 cm., the cortical strip would shrink to 46 cm., and the pith suddenly lengthen to 60-70 cm.

According to J. C. MÜLLER a pressure of 13½ atmospheres would be needed to prevent the expansion of the isolated pith.

From this experiment it will be seen that the natural length of a stem represents the equilibrium maintained between the tendency of the pith to elongate and of the outer tissues to contract. The cortical tissue between the epidermis and the pith affords a transition between the two extremes of tension, the inner cell layers are compressed like the pith, and the outer layers stretched like the epidermis. The tension of tissues is also demonstrated by the fact that each strip of a fresh shoot which has been split longitudinally will curve outward, so that the pith forms the convex, the epidermis the concave side.

There is often a great difference in tension even between the outer and inner layers of the tissue of hollow organs, such as the stalks of a Dandelion (*Taraxacum officinale*), which, when split longitudinally, curl into helices of many turns, especially if placed in water. A tension exists wherever resistant and unequally strained tissues are in contact, and often occurs in parts of plants where it does not assist, as in the leaves and stems, in maintaining the rigidity of the plant body. Longitudinal and transverse tensions occur, particularly when, through secondary growth, newly formed growing tissues have to overcome the resistance of other tissues. In this way the primary and later the secondary cortex of trees become greatly stretched by the new cambial growth, so much so, that if a ring of bark be removed from a stem and then placed round it, a force of ten atmospheres is needed to make the edges meet; this was shown by an experiment of KRABBE.

In the meristematic tissues of growing points there is scarcely any perceptible tension, while, on the other hand, in regions which are in a state of elongation the tension of the tissues attains its highest limit. After an organ has completed its growth the elasticity of the cell walls and the turgescence of the cells decrease; and the tension of the tissues is therefore also diminished. The requisite rigidity is, however, now provided for by special groups of cells with thickened and hardened walls, which thus constitute a firm framework for the other tissues similar to the bony skeleton of the higher animals.

Mechanical Tissues (Stereome) (4).—The supporting framework of plants is provided by the thick-walled elements of the wood, the thickened sclerenchymatous fibres of the fundamental tissue and the bast, and more rarely by groups of stone-cells. The firm thick walls of these tissues are not infrequently further hardened by deposits of mineral substances. The resistance which these forms of tissue offer when the attempt is made to cut, tear, or break them affords sufficient evidence of their hardness, tenacity, and rigidity. Moreover, SCHWENDENER has been able to determine their mechanical value by means of exact physical experiments and investigations. According to such estimates, the sustaining strength of sclerenchymatous fibres is, within the limits of their elasticity, in general equal to the best wrought iron or hammered steel, while at the same time their ductility is ten or fifteen times as great as that of iron. It is true that soon after exceeding its limit of elasticity the stereome of the plant becomes ruptured, while the modulus of rigidity for iron is not reached until the load is increased threefold. It is, however, of value for the needs of the plant that its limit of elasticity extends almost to the limit of its rigidity.

Just as the mechanical tissues of the internal framework of plants exhibit the physical properties most essential for their purpose, their arrangement, as SCHWENDENER showed, will also be found equally well adapted to the various ends in view, according as they may be required to withstand the strain of flexure, traction, or pressure. To withstand bending, and to offer the utmost possible resistance to it, a peripheral disposition of the rigid mechanical tissue is the most favourable. When a straight rod (Fig. 175) is bent, the convex side elongates and the concave side contracts, that is, the outer edges (*a*, *a* and *a'*, *a'*) are exposed to the greatest variations in length, while, nearer the centre (*i*, *i* and *i'*, *i'*) the deflection and consequent variations in length are less. Accordingly, if the supporting skeleton of a plant stem be placed near the centre (*i*, *i'*), then a considerable degree of curvature is possible with but little flexure of the mechanical tissue. Nearer the periphery it would be subject to greater strain, and so offer a greater resistance to the deflecting force. It is essential that the girder-like arrangement of the stereome should be held together by a connecting tissue which is at once resistant and elastic. In the absence of such connecting tissue, the place of which in hollow members may, however, be taken by firm tangential connection of the mechanical tissues, the individual ribs of stereome are easily bent (Fig. 175, 2). In erect stems and flower-stalks where rigidity is an essential requirement, the mechanical tissue is situated at the periphery, and often takes the form of projecting ridges (Fig. 176, 1, 2).

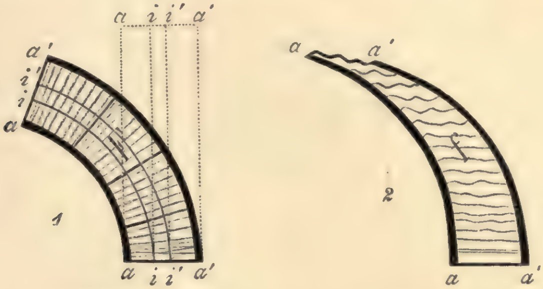


FIG. 175.—1. Longitudinal section of an elastic cylinder, before bending (dotted outline) and after bending (heavy outline). After bending the convex side (a') is stretched and the concave side (a) compressed. *F*, connecting tissue.

2. When the connecting tissue (f) is not sufficiently firm, the bands of stereome (a, a') curve independently and remain unaltered in length.

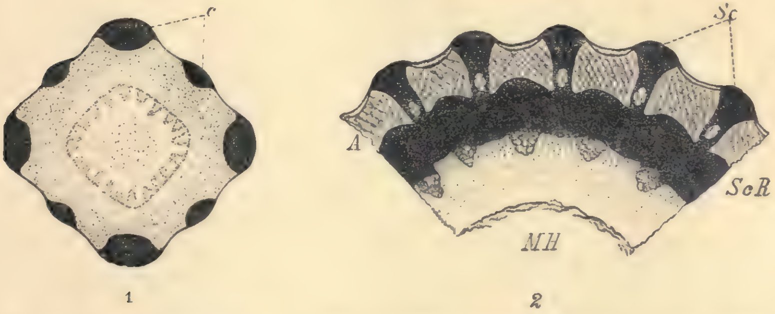


FIG. 176.—Rigidity against bending. 1. Transverse section of a young twig of *Sambucus*; *c*, collenchyma. 2. Part of the transverse section of a haulm of grass (*Molinia coerulea*); *sc*, ribs of sclerenchyma; *sc R*, sclerenchymatous ring connecting them laterally; *A*, green assimilatory tissue; *MH*, pith-cavity.

In roots, and in many rhizomes and stolons, which must push between impeding obstacles, the skeletal system is central, where without interfering with the bending, it can more effectually sustain strains upon the longitudinal rigidity of the organ by being thus massed together (Fig. 177). The stereome is more highly developed in those roots which mainly serve to attach the plant to the substratum than in those the main duty of which is to absorb food material (⁵).

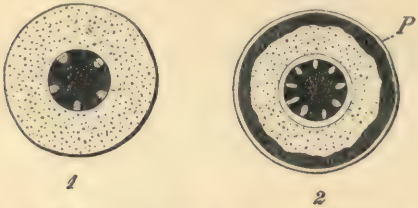


FIG. 177.—Mechanical tissue of roots. 1, Centrally placed to resist longitudinal pulling strains; 2, a prop root with a peripheral layer of mechanical tissue (*P*) to resist lateral pressure, in addition to the central strand.

Where, however, pressure must be guarded against (as in Plum-stones, and in Hazel-nuts and Walnuts), and also in some subterranean or submerged parts of plants, the mechanical resistance is maintained by an arching mass of sclerotic cells or sclerenchymatous fibres.

Stems of trees which have to support heavy and frequently large crowns, must, like pillars, be constructed to withstand the longitudinal pressure as well as the bending.

Leaf-blades must be strengthened not only against bending forces, but against tearing of their expanded surface by the action of wind or currents of water. The former requirement is met by the vascular bundles which often project as ribs on the lower surface, and by girder-like arrangements of the stereome (*Phormium tenax*, Fig. 178, 1). Protection against tearing forces is mainly afforded by the firmness of the margin of the leaf; this is partly attained by the vascular bundles forming marginal arches or running parallel to the margin, in part by special marginal strands of stereome (Fig. 178, 2). Where, as in the Banana, both these means of protection are wanting, the lamina is regularly and easily torn by the wind.

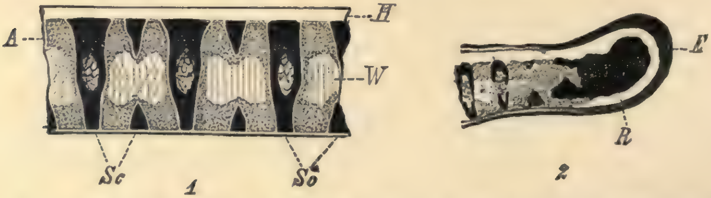


FIG. 178.—Leaf of *Phormium tenax*. 1. Transverse section; *Sc*, plates and strands of sclerenchyma; *A*, green assimilatory parenchyma; *H*, hypoderma serving for water-storage; *W*, colourless mesophyll (internal water-storage tissue). 2. Edge of the same leaf; *E*, thick brown epidermis; *R*, marginal strand of sclerenchyma fibres.

Collenchyma.—All such strongly thickened, inflexible skeletal elements have lost their capacity for growth, and cannot, therefore, be utilised in those parts of plants which are in an actively growing state. In such cases when further support is required than is afforded by turgidity and tissue tension, it is secured by the development of COLLENCHYMA (p. 68). In spite of the amount of water it contains, this tissue, according to AMBRONN'S researches, opposes considerable resistance to tearing, while it is easily stretched by a longitudinal pull. When the part of the plant containing it is growing more or less actively, the collenchyma thus readily accommodates itself to the change in form. It forms, so to speak, the cartilaginous tissue of plants (6).

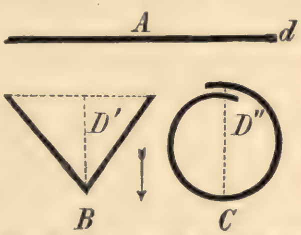


FIG. 179.—Diagrammatic transverse sections, to show method of securing rigidity by folding and rolling. In the outspread organ *A*, to withstand a pressure acting in the direction of the arrow, only the thickness *d* is available, but in the folded organ *B* the thickness *D'*, and in the rolled organ *C* the thickness *D''*.

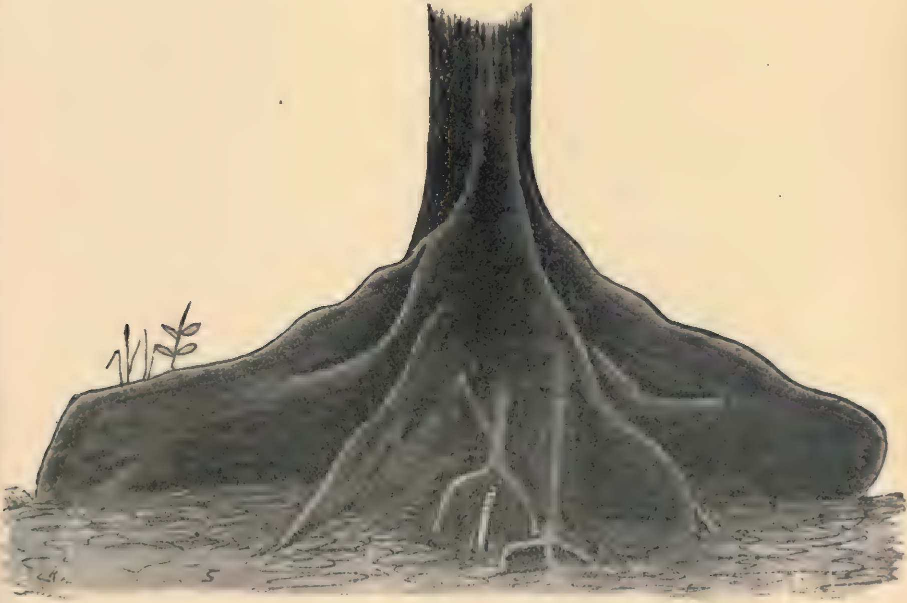


FIG. 180.—Buttress roots of a species of *Sterculia*. (After HABERLANDT: from SCHIMPER'S *Plant-Geography*.)

Since, as has already been pointed out, the resistance of the mechanical elements to flexure is greater the farther they are removed from the centre of an organ, it will be readily seen that, while a flattened, outspread organ can be easily bent, its power of resisting a deflecting force would be increased if it were folded or rolled together. In accordance with this principle many leaves become plaited or rolled (Fig. 179), and so acquire a sufficient rigidity without the assistance of any specially developed mechanical tissues.

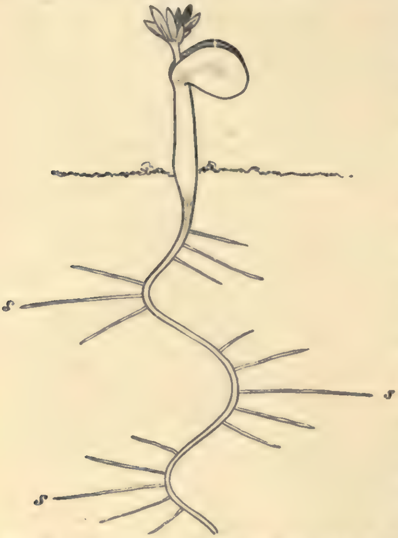


FIG. 181.—Young plant of Lupine, the main root of which has become curved. The lateral roots have arisen on the convex faces of the curves, and act as stays.

In addition to the rigidity of the individual organs of the plant, their arrangement and position are of importance for the stability of the whole organism. The lateral branches, which are normally arranged as symmetrically as possible, may be forced by bending them upwards or downwards to take on an elliptical cross-section or to form knee-like bends. In Conifers the "white wood," which offers greater resistance to stretching forces, and the "red wood," which being denser offers greater resistance to compression, are formed on the sides which are respectively stretched or compressed (7). The roots of many tropical trees are so excentrically constructed as to form relatively thin plank-like buttresses to the trunk (Fig. 180).

Lateral roots originate from the convex flanks of a main root which has been thrown into curves (Fig. 181), and act as stays, preventing the straightening of the root and the loosening of the hold of the root-system which would result from this (8).

II. Nutrition

By nutrition are understood all the processes of METABOLISM, or the chemical transformation and conversion of matter carried on by plants in the production and appropriation of their food supply. Without nourishment and without the supply of new formative material neither growth nor development is possible, nor, indeed, without continuous nutrition can a plant maintain itself in any given stage of its development. The processes of life are connected with constant changes of the living substance, both transformations and excretions. Even when the supply of food ceases these processes continue, so that the death of the organism from starvation must ensue if the substances that are used up are not at least replaced in the process of nutrition.

The Constituents of the Substance of the Plant.—By means of chemical analysis the constituent substances of plants can be most accurately ascertained. It requires, however, no analysis to realise that a part, often indeed the greater part, of the weight of a plant is derived from the water with which the whole plant is permeated. Water not only fills the cavities of living, full-developed cells, but it is also present in the protoplasm, cell walls, and all organised structures. By drying at a temperature of 110°-120° C. all water may be expelled from vegetable tissues, and the solid matter of the plant will alone remain. The amount of dried substance in plants varies according to the nature and variety of the plant and of the particular organ. In woody parts it constitutes up to 50 per cent of their weight, but in herbaceous plants amounts to only 20 or 30 per cent. In succulent plants and fruits it makes up only 5-15 per cent of their total weight; in water-plants and Algae, 2-5 per cent, while all the rest is water.

The dried substance of plants is combustible, and consists of organic compounds, which contain but little oxygen, and are converted by combustion into simple inorganic compounds, for the most part into carbonic acid and water. The elements CARBON, HYDROGEN, and OXYGEN form the chief constituents of the combustible dried substance. Next to them in quantity is NITROGEN, which is derived principally from the protoplasm. After combustion of the dried substance of plants there always remains an incombustible residue, the ASH, consisting of the mineral substances contained in the plant. As these mineral substances undergo transformation during the process of combustion, they are found in the ash in chemical combinations different from those in living plants. From numerous analyses made of the ash of a great variety of plants, it has been determined that nearly all the elements, even the rarer ones, may be present in plants.

In addition to the four already named, the elements met with in the ash of plants are sulphur, phosphorus, chlorine, iodine, bromine, fluorine, selenium, tellurium, arsenic (which may be combined as a superphosphate in the soil), antimony, silicon, tin, titanium, boron, potassium, sodium, lithium, rubidium, calcium, strontium, barium, magnesium, zinc, copper, silver, mercury, lead, aluminium, thallium, chromium, manganese, iron, cobalt, and nickel.

Many of these elements, indeed, occur only occasionally and accidentally, while others — sulphur, phosphorus, chlorine, silicon, potassium, sodium, calcium, magnesium, and iron—are met with in almost every ash. As might be inferred from the irregular occurrence of many of the elements, they are not all necessary for nutrition, and although their occasional presence in a plant may sometimes change certain of its special characteristics (thus the presence of zinc produces the so-called calamine varieties, for example, *Thlaspi alpestre* var. *calaminare*, *Viola lutea* var. *calaminaria* (Fig. 182), etc.), they do not exercise a decisive influence upon its existence.

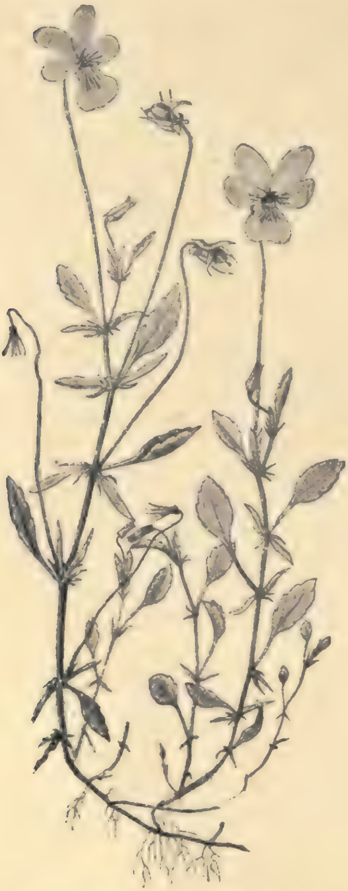


Fig. 182. — *Viola lutea* var. *calaminaria*, which has longer stems, smaller flowers, and is more branched than the type form. (½ nat. size, from Schimper's *Plant-Geography*.)

The Essential Constituents of Plant Food. — Chemical analysis, while enabling us to determine the substances present in plants, does not show how far they are essential for nutrition. From culture experiments, in which the plants are grown in a medium of which the constituents are known, and kept under chemical control, it has been ascertained that, in addition to **carbon, hydrogen, oxygen,** and **nitrogen,** which form the principal part of the combustible elements of the dry substance of plants, **sulphur, phosphorus, potassium, calcium, magnesium,** and **iron** are absolutely indispensable to the growth of all green plants. In the absence of even a single one of these elements no normal development is possible.

According to Molisch, only nine of these elements are required by the Fungi. It is not, however, iron, as might be supposed, but either calcium or magnesium, that is unessential. On the other hand, the ten substances named suffice for the nutrition of most green plants; but it is not to be denied that certain other substances are of use in the plant economy and of advantage to growth, although not indispensable. Thus, for example, Buckwheat flourishes better when supplied with a chloride, and the presence of silica is advantageous as contributing to the rigidity of the tissues.

It has also been discovered that by the presence of certain substances, in themselves of no nutritive value, the absorption of actual nutritive matter is increased. In minimal doses poisonous substances often have a favourable effect; they lead to better utilisation of the substances at the disposal of the plant and increase the "economic co-efficient." Their effect is, however, often injurious even when diluted so as to be imperceptible to chemical tests; thus by such "oligodynamic" influence copper sulphate, even in the proportions of 1:25,000,000, has a fatal effect on *Spirogyra*, and on Peas in a water culture (⁹).

The nutritive substances are, naturally, not taken up by plants as elements, but in the form of chemical compounds. CARBON, the essential component of all organic substances, is obtained by all green plants solely from the carbonic acid of the atmosphere, and is taken up by the leaves. All the other constituents of the food of plants are drawn from the soil by the roots. HYDROGEN, together with OXYGEN, is obtained from water; oxygen is derived also from the atmosphere and from many salts and oxides. NITROGEN is taken up by the higher plants only in the form of nitrates or ammonium salts; certain Fungi, Algae, and carnivorous plants, however, obtain it in the form of peptone, amido-acids, amides, or even urea. As the ammonia of the soil formed by the soil bacteria from organic decaying matter is transformed by the help of other so-called nitrifying bacteria into nitrites, and eventually into nitrates, only the nitrogen combined in the nitrates need be taken into consideration (¹⁰).

Bacteria, as contrasted with the higher plants, are particularly characterised by their attitude towards nitrogen. In addition to the bacteria, which, by their nitrifying capability, are of service to green plants, there are other soil bacteria which in presence of organic compounds of carbon set free the nitrogen of nitrogenous compounds, and thus render it unserviceable for the nutrition of green plants. On the other hand, other forms of bacteria (*e.g. Azotobacter chroococcum*, *Clostridium pasteurianum*), other species of the same group of bacteria, and sometimes also mixtures of certain soil bacteria (¹¹) convert the free nitrogen of the air into compounds which serve not only for themselves, but also for other organisms in the soil and for the higher plants as nitrogenous food material. Whether some Fungi have the same power is still an unsettled question. From the comparison of the crops obtainable from plots of land with and without the addition of manure, J. KUHN has concluded that a very considerable fixation of nitrogen takes place in the soil; according to WORMBOLD this is in part independent of the action of micro-organisms (¹²).

SULPHUR and PHOSPHORUS form, like nitrogen, important constituents of protoplasm. All proteid substances contain ½-2 per cent of sulphur. The sulphur is taken into plants in the form of sulphates; phosphorus in the form of phosphates. POTASSIUM, unlike sodium, is essential to plant life, and is presumably active in the processes of assimilation and in the formation of protoplasm; it is introduced into plants in the form of salts, and constitutes 3-5 per cent of the weight of their dried substance. MAGNESIUM, like potassium participating in the most important synthetic processes of plants, is found in combination with various acids, particularly in reservoirs of reserve material (in seeds to the extent of 2 per cent) and in growing points (in leaves only ½ per cent). Calcium also is taken up in the form of one of its abundant salts, and in considerable quantities (2-8 per cent). Calcium plays an important part in the metabolic processes of plants, as a vehicle for certain other essential substances, and, as a means of fixing and rendering harmless hurtful bye-products (oxalic acid)(13). Iron, although of the greatest importance in the formation of chlorophyll, is present in plants only in small quantity.

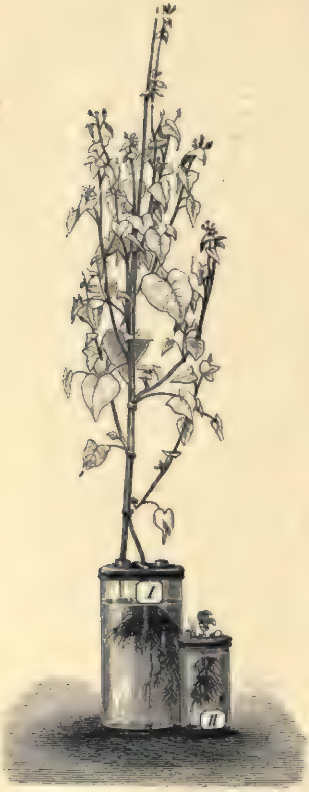


Fig. 183.—Water-cultures of *Fagopyrum esculentum*. *I.* In nutrient solution containing potassium; *II.*, in nutrient solution without potassium. Plants reduced to same scale. (After Nobbe.)

In order to determine the nutritive value of different substances the method of water-culture has proved particularly useful (Fig. 183). In these culture experiments the plants, grown either directly from the seed or from cuttings, are cultivated in distilled water to which have been added certain nutritive salts. The distilled water must not have been stored in a copper vessel, and the salts must be chemically pure. If all the essential nutritive salts are present in the culture solution, even larger plants, such as Indian Corn, Wheat, Beans, etc., will grow to full strength and mature seeds as if grown in earth. It is not necessary in these experiments to provide carbon compounds in the nutrient solution, as plants do not derive their carbon supply through their roots, but, by the help of their leaves, from the carbonic acid of the atmosphere.

The young plants grow for a time just as well in pure distilled water as in the nutrient solution; but as the supply of nourishment stored in the seeds becomes exhausted, they gradually cease to grow, and die. If one of the essential constituents of plant food be omitted from the nutrient solution, although the young plants will grow better than in the distilled water, they in time become abnormally developed. When, for example, a plant is grown in a nutrient solution containing all the essential food elements except iron, the new leaves developed are no longer green, but are of a pale yellow colour; they are "CHLOROTIC," and not in a condition to decompose the carbonic acid of the atmosphere and nourish the plant. Upon the addition, however, of a mere trace of iron to the solution the chlorotic leaves in a very short time acquire the normal green colour. The chlorophyll, however, does not contain iron, but always contains magnesium.

So long as the necessary nutritive substances are provided, the form in which they are offered to the plants, as well as the proportionate strength of the nutrient solution (if not too concentrated), may vary. Plants have the power to take up these substances in very different combinations, and are able to absorb them in other proportions than those in which they occur in the soil. In concentrated nutrient solutions the absorption of water is increased; conversely, in very dilute solutions it is the salts that are chiefly taken up. The presence also of certain substances often exerts an active and generally beneficial influence upon the capacity for absorbing other substances: thus, calcium salts increase the absorption of potassium and ammonium salts. Calciphobous plants do not succeed on soil rich in lime either because the absorption of potassium, magnesium, and iron is greatly interfered with (*Castanea*, *Sarothamnus*), or because the calcium exercises a poisonous effect (*Pinus pinaster*, *Sphagnum*, *Drosera*). Other plants are calcicolous and succeed best with a high percentage of lime in the soil.

In order to avoid the poisonous effects of phosphates and salts of iron, when supplied in a soluble form, v. d. Crone recommends the following nutritive solution:—

Distilled water	1-2 litres.
Potassium nitrate	1·0 gramme.
Ferrous phosphate	0·5 ,,
Calcium sulphate	0·25 ,,
Magnesium sulphate	0·25 ,,

A mixture of equal parts of ferrous phosphate and tri-calcic phosphate may be used in place of the ferrous phosphate in the above formula. The phosphates which are present as a fine powder in the solution become deposited on the surface of the roots of plants growing in the fluid. Plants are found to grow better in the above solution than in those used by Knoop and Sachs. The growth of Algae is hindered in this solution (14).

As a most important result of such culture experiments, it has been demonstrated that only the ten elements already named are necessary for the growth of plants; all other elements, although present in plants in large quantities, are of subordinate value to plant life. This is true, for instance, of SODIUM, which, in combination with CHLORINE, actually predominates in some plants, and occasions the characteristic development of many of the succulent salt-plants (halophytes); and also of SILICON, which, as silica, is so abundantly deposited in the cell walls of many plants—Equisetaceae, Grasses, Sedges, Diatoms (in the ash of Wheat-straw 70 per cent, and of Equisetaceae 70-97 per cent)—that, after combustion of their organic substances, it remains as a firm siliceous skeleton, preserving the structure of the cell walls. The hardness and firmness of the cell walls are greatly increased by these siliceous deposits; they themselves have about the degree of hardness 2, but the silicified epidermis of *Equisetum* has the hardness 4 (= Fluorspar), and that of the fruits of *Coix* 7 (= Quartz). Some of the Equisetaceae are even used for polishing and scouring. The silicified cell walls of Diatoms occur as fossils, and form deposits of **SILICEOUS EARTH** (Kieselguhr) in some geological formations. The value of the siliceous concretions, termed "tabasheer," that are found within the joints of the Bamboo has not, as yet, been satisfactorily explained. **ALUMINIUM**, although like silica everywhere present in the soil, is only in exceptional instances taken up by plants (Lycopodiaceae, Lichens, Vitaceae, Leguminosae). Some species of *Lycopodium* contain a sufficient quantity of acetate of aluminium to render the sap useful as a mordant. The same salt is found also in Grapes. On the other hand, although scarcely a trace of iodine can be detected by an analysis of sea-water, it is found, nevertheless, in large quantities in seaweeds, so much so that at one time they formed the principal source of our supplies of this substance (15).

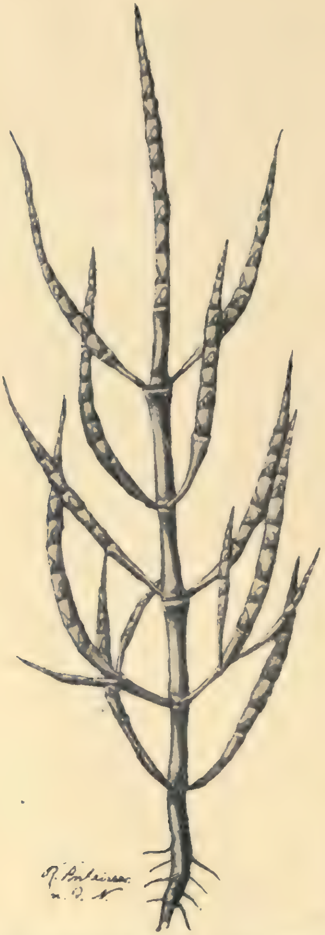


Fig. 184.—*Salicornia herbacea*, a characteristic halophyte. (From Schimper's *Plant-Geography*.)

The substances which, as culture experiments show, are not indispensable for the life of the plant are, however, of use in so far as they can replace for some purposes (such as the neutralisation of free acids, etc.) essential elements of plant food. The latter are thus available for the special purposes for which they are indispensable. Thus K can be partially replaced by Na, and Mg by Ca.

It was first asserted by Berthollet (1803), and afterwards emphasised by Liebig and C. Sprengel, that the mineral salts contained in plants, and once supposed to be products of the vital processes of the plants themselves, were essential constituents of plant food. Conclusive proof of this important fact was, however, first obtained by the investigations of Wiegmann and Polstorff (16).

The actual proportions of the more important ash constituents of some well-known plants can be seen from the following table of ash analysis by E. Wolff (17). The table also shows exactly what demands those plants make upon the soil, that is, what substance they take away from it, in addition to the nitrates which do not appear in the ash.

Plants.	Ash in 100 parts of dry solid matter.	100 Parts of Ash contain									
		K_2O	Na_2O	CaO	MgO	Fe_2O_3	Mn_3O_4	P_2O_5	SO_3	SiO_2	Cl
Rye (grain) . .	2·09	32·10	1·47	2·94	11·22	1·24	. .	**47·74**	1·28	**1·37**	0·48
Rye (straw) . .	4·46	22·56	1·74	8·20	3·10	1·91	. .	**6·53**	4·25	**49·27**	2·18
Pea (seeds) . .	2·73	43·10	0·98	**4·81**	7·99	0·83	. .	**35·90**	3·42	0·91	1·59
Pea (straw) . .	5·13	22·90	4·07	**36·82**	8·04	1·72	. .	**8·05**	6·26	6·83	5·64
Potato (tubers) .	3·79	60·06	2·96	2·64	4·93	1·10	. .	16·86	6·52	2·04	3·46
Grape (fruit). .	5·19	56·20	1·42	10·77	4·21	0·37	. .	15·58	5·62	2·75	1·52
Tobacco (leaves)	17·16	29·09	3·21	36·02	7·36	1·95	. .	14·66	6·07	5·77	6·71
Cotton (fibres) .	1·14	39·96	13·16	17·52	5·36	0·60	. .	10·68	5·94	2·40	7·60
Spruce (wood) .	0·21	19·66	1·37	33·97	11·27	1·42	**23·96**	2·12	2·64	2·73	0·07

The great difference brought out by the table in the proportions of the more important phosphoric acid and of the less essential silica and lime contained in Rye and Pea seeds, as compared with the amounts of the same substances in the straw, is worthy of especial notice.

In a similar way the marine Algae, according to Wille (18), economise the nitrates and phosphates, which exist in small proportions in sea-water, but not potassium and magnesium, the supply of which is abundant.

In the preceding table the figures do not express absolutely constant proportions, as the percentage of the constituents of the ash of plants varies according to the character of the soil; thus, the proportion of potassium in Clover varies from 9 to 50 per cent; the proportion of calcium in Oats from 4 to 38 per cent.

The Process of Absorption (19).—As all matter absorbed by plants must, as a rule, pass through continuous cell walls, no solid food can be taken up. The only exception to this rule occurs in the amœboid developmental stages of the lower plants (amœbæ and plasmodia), which, as they have no cell walls, are in a condition to take up and again extrude solid matter (particles of organic or inorganic substances).

The fact that plant cells are completely enclosed by continuous walls renders it necessary that food, to pass into the cell, must be either liquid or gaseous. In this condition the constituents of plant food are, however, imperceptible, and thus the manner of plant nutrition remained for a long time a mystery, and it was only during the eighteenth century that the nature of the nourishment and nutritive processes of plants was recognised.

The nutrition of the plant is dependent upon the permeability of the cell walls to liquids and gases. Although impervious to solids, the cell walls of living cells are permeated with "imbibed" water; and to this "IMBIBITION WATER" in the cell walls, together with the physical character of the cell walls themselves, are due their flexibility, elasticity, and extensibility. The permeability of cell walls for imbibition water is only possible within certain limits, so that they thus retain the character of solid bodies.

Treated with certain chemical reagents (potassium hydrate, sulphuric acid, etc.) cell walls become swollen and gelatinous, or even dissolve into a thin mucilaginous slime. This change in their character is due to an increase in the amount of their imbibition water, induced by the action of the chemicals; otherwise, the water imbibed by ordinary cell walls is limited in amount. The walls of woody cells take up by imbibition about one-third of their weight; the cell walls of some seeds and fruits and of many Algae absorb many times their own volume when dry.

THE CELL WALLS ARE NOT ONLY PERMEABLE TO PURE WATER, BUT ALSO TO SUBSTANCES IN SOLUTION. This fact, that the cell wall offers no resistance to the diffusion of crystalloid bodies when in solution, is of the utmost importance for the nutrition of the plant; cell walls, on the other hand, which are scarcely or not at all permeable to liquids (cuticularised walls), take no part in the absorption of plant-nourishment, except in so far as they may still be permeable to gases.

In order that liquids may enter by osmosis into the living cell, they must first pass through the protoplasm, and in the first place through the outer limiting membrane of the protoplast which is in contact with the cell wall. LIVING PROTOPLASM is not, however, like the cell walls, equally permeable to all substances in solution, but, on the contrary, COMPLETELY EXCLUDES CERTAIN SUBSTANCES WHILE ALLOWING OTHERS TO PASS THROUGH MORE OR LESS READILY. Moreover, it is able to change its permeability according to circumstances, and thus THE OUTER PROTOPLASMIC MEMBRANE HAS THE POWER OF DECISION whether a substance may or may not effect an entrance into the cell. The wall of the vacuole exercises a similar but often quite distinct power over the passage of substances from the protoplasm into the cell sap. The same influence is exercised by these membranes on the transfer of substances in a reverse direction. On account of the selection thus exercised by the protoplasm, the contents of a cell, in spite of continued osmotic pressure, are often of quite a different chemical nature from the immediately surrounding medium. To this same peculiar quality of the protoplasmic membranes is also due the SELECTIVE POWER of cells, manifested by the fact that different cells, or the roots of different plants, appropriate from the same soil entirely different compounds; so that, for instance, one plant will take up chiefly silica, another lime, a third common salt. The action of Seaweeds in this respect is even more remarkable; living in a medium containing 3 per cent of common salt, and but little potassium salts, they nevertheless accumulate much larger quantities of potassium than sodium. In addition they store up phosphates, nitrates, and iodine,—substances which are all present in sea-water in such small quantities as scarcely to be detected by chemical analysis. *Penicillium glaucum* is able to grow on a nutritive solution containing 21 per cent of sulphate of copper, owing to the power it possesses of allowing the entrance to the cell of the salts it requires, while preventing that of the copper sulphate (^{20}).

That osmosis may continue into a cell, it is essential that the absorbed material should become transformed into something else, either by the activity of the protoplasm or by some other means. Local accumulations of sugar or other soluble reserve material in fruits, seeds, bulbs, and tubers would otherwise not be possible; for osmotic action, if undisturbed, must in the end lead to the uniform distribution of the diffusible substances equally throughout all the cells. But if equilibrium is prevented by the transformation of the diffusible substances into others that are indiffusible, the osmotic currents towards the transforming cells will continue, and the altered and no longer diffusible substances will be accumulated in them. In this manner glucose passing by osmosis into the cells of tubers or seeds becomes converted into the insoluble polysaccharide, starch. As a result of this a constant movement of new glucose is maintained towards these cells, which thus become reservoirs of accumulated reserve material.

Water and Mineral Substances

Without water there can be no life. THE LIVING PORTIONS OF ALL ORGANISMS ARE PERMEATED WITH WATER; it is only when in this condition that their vital processes can be carried on. Protoplasm, the real physical basis of life, is, when living, of a viscous, thinly fluid consistency, and when dried either dies or becomes inactive.

Protoplasm, when in a state of inactivity, as in spores and seeds, can often endure a certain degree of desiccation for a limited time. During such periods its actual vital functions cease, and only renew their activity when water is again supplied.

With the exception of some succulent plants which are uninjured by the loss of nine-tenths of their water, plants as a rule have their activity impaired by the loss of water in withering and are killed by complete desiccation. It is always to be regarded as due to some special provision or exceptional quality when entire plants or their reproductive bodies which have been dried can be again brought to life by a supply of water. Thus, for example, some Algerian species of *Isoetes* and the Central American *Selaginella lepidophylla* can withstand droughts of many months' duration, and on the first rain again burst into life and renew their growth. In like manner many Mosses, Liverworts, Lichens, and Algae growing on bare rocks, tree-trunks, etc., seem able to sustain long seasons of drought without injury.

Seeds and spores, after separation from their parent plants, remain productive for a long time; seeds of *Nelumbium*, which had been kept dry for over one hundred years, proved capable of germination. A similar vitality was shown by moss spores which had lain in a herbarium fifty years. The often-repeated assertion concerning the germination of wheat found with Egyptian mummies ("mummy-wheat") has, however, been shown to be erroneous. Many seeds lose their power of germination after having been kept dry for only a year; others, even after a few days; and others again cannot endure drying at all. On the other hand, the seeds of some water plants (*Eichhornia*, etc.) germinate better after being dried for a period. It must not be forgotten that in all these instances a certain amount (about 9-14 per cent) of hygroscopic water is retained by plants even when the air is quite dry. Over the sulphuric acid of the desiccator, seeds retain for weeks 6 per cent or more of their weight of water. Even drying at 110° or the action of absolute alcohol can be borne by some spores and seeds (21).

Apart from permeating and energising the cells, water has other and more varied uses in plant life. It is not only indirectly indispensable for the solution and transport of the products of metabolism, but also directly in that its elements, hydrogen and oxygen, are made use of in the formation of organic compounds in plant nutrition. Water thus used (cf. p. 219) may be designated CONSTITUTION WATER; for example, in the formation of every 100 grammes of starch or cellulose 55 grammes of constitution water, and in the formation of the same amount of glucose 60 grammes of water, are used. Water is also necessary for the turgidity and consequent rigidity of parenchymatous cells (p. 179); it is of use in the process of the growth of plant cells, which take it up in large quantities, and, through their consequent expansion, enlarge their volume with but little expenditure of organic substance.

A further and still more important service which water performs for plants consists in THE CONVEYANCE AND INTRODUCTION INTO THE PLANT BODY OF THE NUTRIENT SUBSTANCES OF THE SOIL. Although a large amount of water is retained in the plant body (up to 96 per cent in succulent tissues) for the maintenance of rigidity and enlargement of the organs, a still larger quantity of the water taken up by the roots passes through the plant merely as a medium for the transport of nourishment, and is again discharged through the leaves by evaporation. By this TRANSPIRATION from the aerial part of plants, the water passing into them from the roots escapes, and at the same time, by preventing saturation, which would otherwise be produced, a continuous upward movement of the water is maintained. The current of water thus produced is accordingly termed the TRANSPIRATION CURRENT. As the result of evaporation only water, in the form of vapour, and gases can escape from the plant. AS THE WATERY FLUID ABSORBED BY THE ROOTS CONTAINS SALTS, AND OTHER NON-VOLATILE SUBSTANCES IN SOLUTION, THESE ON EVAPORATION ARE LEFT IN THE PLANT AND GRADUALLY INCREASE IN QUANTITY. This accumulation of mineral salts is absolutely necessary for the plant, for the nutrient water taken up by the roots is so weak in mineral substances (it contains but little more solid matter than good drinking-water), that the plant would obtain too little food if it were only able to take up as much water as it could retain and make use of.

ALL THOSE CONTRIVANCES, IN PLANTS, THEREFORE, WHICH RENDER POSSIBLE OR PROMOTE EVAPORATION, OPERATE CHIEFLY IN THE SERVICE OF NUTRITION. Were transpiration not in the highest degree useful and even necessary for the acquisition of mineral substances, provision would certainly have been made by plants to restrict it within the narrowest possible limits. For transpiration increases the amount of water required by plants disproportionally to their powers of absorption, and exposes them, moreover, to the danger of perishing through the insufficiency of their water-supply. In spite of the increased danger of drying up, as the result of evaporation, special provision is made by plants for facilitating transpiration (p. 205).

The Absorption of Water.—The "water" absorbed by the plant is not chemically pure water, but a DILUTE WATERY SOLUTION OF VARIOUS SUBSTANCES FROM THE SOIL AND FROM THE ATMOSPHERE. Through the peculiar selective power of their cells (p. 194) plants exercise a choice from among the substances available in the nutrient solution.

Aquatic plants and the lower land-plants which are but little differentiated, such as the Mosses, can absorb water by their general surface. The same is true of many aquatic Phanerogams. These (*Utricularia*, *Ceratophyllum*, *Wolffia*), like some Hymenophyllaceae of damp primæval forests, the epiphytic *Tillandsia usneoides* and the Sundew, possess as a rule no roots. The roots of many submerged plants, on the other hand, penetrate the soil and contribute essentially to the nutrition of the plant.

In plants living on dry land the conditions are quite different; their stems and leaves develop in the air, and they are restricted to the water held by capillarity in the soil. In order to obtain this water in sufficient quantities, special organs are necessary, which may spread themselves out in the soil, and enter into intimate connection with its particles, in their search for water. These organs must absorb the water from the soil, and then force it to the aerial portions of the plant. This office is performed for a land plant by its root system, which, in addition to providing the supply of water, has also the task of mechanically fastening the plant in the soil (22).

Conversely, loose soil is naturally bound together by the branching roots; and on this account plants have an economic value in holding together loose earth, particularly on dykes and land subject to inundation.

The small clod of earth, that is as a rule at the disposal of a plant in its natural habitat, is utilised to the full by the highly developed root system, which behaves in a wonderfully purposive manner.

If the development of the root system of a germinating Bean or Oak be observed, it will be found that the growing root of the embryo at once penetrates the soil and pushes straight downwards. Lateral roots are then given off from the main axis, and, growing either horizontally or diagonally downwards, penetrate the earth in the neighbourhood of the primary root. These lateral secondary roots in turn develop other roots, which radiate in all directions from them, and so occupy and utilise the entire soil at their disposal. The branching of the root system can proceed in this manner until, within the whole region occupied by the roots of a large plant, there is not a single cubic centimetre of earth which is not penetrated and exhausted by them. The system of branches of one root system often has an astonishingly great total length, and may amount to ½ a kilometre in an annual cereal, and to several kilometres in a well-developed *Cucurbita*.

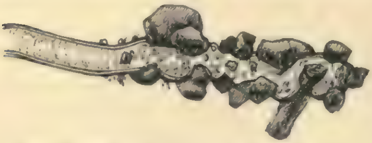


FIG. 185.—Tip of a root-hair with adhering particles of soil. (× circa 240.)

All plants do not form a deep-growing tap-root like that of the Oak, Silver Fir, Beet, Lucerne, etc. ; some confine themselves to utilising the superficial layers of the soil by means of a thickly branched lateral root system (Pine, Cereals). The agriculturist and forester must, accordingly, take into consideration the mode of branching and growth of the roots of a plant just as much as the habit of growth of its aerial portions. Plants which make use of different layers of soil may be safely cultivated together in the same soil, and succeed one another in the same ground. For similar reasons, in setting out trees along the borders of fields, the deep-rooted Elm should be preferred to the Poplar, whose roots spread out near the surface.

Desert or xerophilous plants, according to the observations of VOLKENS, send out deeply penetrating roots, which only branch profusely on reaching depths where they find water. When grown in moderately dry soil the growth of the roots of oats is greater than when the soil is damp.

In order to secure a still more intimate contact with the particles of the soil, there are produced from the surface of roots small, exceedingly numerous, and fine cylindrical bodies, which penetrate the smallest interstices of the soil, and fasten themselves so closely to its smallest particles as to seem actually grown to them (Fig. 185). These ultimate branches of the root system, which discover the very smallest quantity of moisture, and seek out the most concealed crevices in the search for nourishment, are the ROOT-

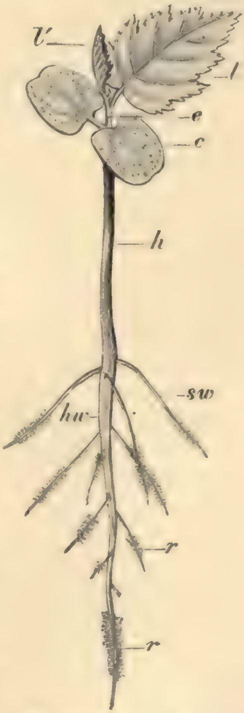


FIG. 186.—Seedling of *Carpinus Betulus*. *r*, Zone of root-hairs near root-tip ; *h*, hypocotyl ; *hw*, main root ; *sw*, lateral roots ; *l*, *l′*, leaf ; *e*, epicotyl ; *c*, cotyledons.

HAIRS,—delicate tubular outgrowths of the epidermal cells. Although they have the diameter of only a medium-sized cell, and appear to the naked eye as fine, scarcely visible, glistening lines, they often attain a length of several millimetres and greatly enlarge the absorbing surface of their parent root. According to F. SCHWARZ the epidermal surface of the piliferous zone of the roots of *Pisum*, which has 230 root-hairs to the square millimetre, is thus increased twelvefold.

The root-hairs cover only a comparatively small zone, a short distance above the growing root-tip. Soon after they have attained their greatest length, and have come into the closest contact with the particles of the soil, they die off. Above this advancing zone of hairs the epidermis of the root becomes again completely divested of root-hairs (Fig. 186). The older parts of roots take no share in the process of absorption. They envelop themselves with cork, increase their conducting elements by growth in thickness, and function exclusively in the transfer of the water absorbed by the younger portion of the roots. Even in the young roots the absorption seems principally confined to the regions covered with root-hairs, or, in case no root-hairs are developed, to a corresponding zone of the root epidermis.

Through the intimate union of the youngest roots with the soil, they are able to withdraw the minute quantity of water still adhering to the particles of earth, even after it appears perfectly dry to the sight and touch. There still remains, however, a certain percentage of water, held fast in the soil, which the roots are not able to absorb. Thus, SACHS found that the water left by a Tobacco plant, and which it could not absorb, amounted in cultivated soil to 12 per cent, in loam to 8 per cent, and in coarse sand to 1½ per cent. Plants may even obtain a certain quantity of water from soil which is frozen hard or from a block of ice.

The ABSORPTIVE POWER of soil depends, partly, upon chemical changes taking place within it, but partly also on physical processes (the superficial adhesive force of its particles). The chemical changes mainly take place in soils rich in clay, lime, or humus, and containing double silicates of alumina. Salts of potassium and ammonium, also those of calcium and magnesium, and phosphates are absorbed by these soils. The former form silicates or double silicates that are only with difficulty dissolved, while the phosphoric acid is held combined with calcium or iron. Magnesium and calcium salts are in other soils but slightly absorbed. They are, like the chlorides, the nitrates, and, in part, also the sulphates, easily displaced; in soil treated with a solution of saltpetre, for example, the potassium will remain in combination in the soil, while calcium nitrate passes off in solution.

Humus acids contribute, to a certain extent, to the chemical changes occurring in soil, as do also soil bacteria, which possess strongly oxidising and reducing powers (cf. p. 189).

The absorptivity of the soil, which, moreover, is not absolute, and varies with different soils (sandy soil absorbs poorly), operates advantageously for plants by the consequent rapid accumulation of large supplies of food-material for their gradual absorption.

The absorptive power of soil for water is due to its capacity to retain water by capillarity, so that it does not drain off. Of the soils investigated by SACHS, cultivated soil retained in this way 46 per cent, loam 52 per cent, and sand only 21 per cent of water.

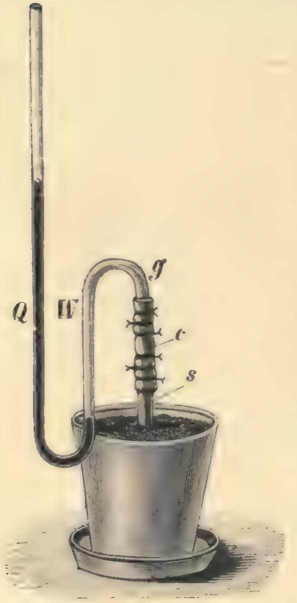


FIG. 187.—Vigorous exudation of water as the result of root-pressure from a cut stem of *Dahlia variabilis*. The smoothly cut stem *s* is joined to the glass tube *g* by means of the rubber tubing *c*. The water *W*, absorbed by the roots from the soil, is pumped out of the vessels of the stem with a force sufficient to overcome the resistance of the column of mercury *Q*.

The young roots, and especially the root-hairs, in addition to the carbonic acid exhaled by them, which, no doubt, aids in loosening the soil, excrete other acid substances which are able to dissolve about the same amount from the soil as is done by a 1 per cent solution of citric acid. Roots growing upon a polished plate of marble, dolomite, osteolith, or even ivory will so corrode them that an etched pattern of the course and direction of the roots is thus obtained. Plants which excrete acid actively (maize, rye, oats) make less demands on a good worked soil than those in which the excretion is less active (wheat, barley) or almost absent (meadow grasses).

The nutrient water with which the cell walls of the epidermal cells and root-hairs first become permeated is taken up by the epidermal cells, and thence passes through the cortical cells and the endodermis to the central cylinder of the root.

The Distribution of the Nutrient Water.—1. ROOT-PRESSURE.—The causes which determine the direction and strength of the movement of the water through the living cells of the root-cortex into the vascular bundles are not yet fully understood. The fact that the water does actually pass into them, and at times indeed is forced into them with a considerable pressure, may be easily demonstrated. If the stem of a strongly growing plant be cut off close above the ground, and the cut surface dried and then examined with a magnifying-glass, water will, in a short time, be seen to exude from the severed ends of the bundles. By close inspection, it is also possible to determine that the water escapes solely from the vessels and tracheides of the bundles. When the soil is kept warm and moist the outflow will be greater, and will often continue for several days and even months. The excreted water may amount to several litres (to 1 litre in the

Vine, 5 litres in the Birch, and 10-15 (50) litres in the Palms). This water, as analysis shows, is not pure, but leaves on evaporation a residue of inorganic and organic substances.

If a long glass tube be placed on the root-stump and tightly fastened by rubber tubing, the exuded fluid will be forced up the glass tube to a considerable height. How great the force of this pressure is may be shown by attaching to the stump a manometer (Fig. 187). The column of mercury will in some cases be forced to a height of 50 or 60, and under favourable conditions to 100 or more centimetres (140 cm. in the Birch). These pressures would be sufficient to raise a column of water 6, 8, and 18 metres high. The height to which the fluid can be raised is the less surprising when the much greater forces due to turgescence, which are at the disposal of living cells, is remembered (23).

If, instead of the effects of the pressure, the volume of water exuded each hour be observed, the remarkable fact will be demonstrated that the roots regularly discharge more water at certain hours than at others (PERIODICITY OF ROOT-PRESSURE). The quantity is greater by night than by day.

When it was shown that the roots were capable of exercising so great a pressure, it was at first believed that the ascent of the sap to the tops of the highest trees was due to root-pressure. This, however, appears impossible in view of the following considerations. The volume of water supplied by root-pressure is not sufficient to replace the quantity given off by evaporation. On the contrary, during moderately vigorous transpiration, such as takes place on a summer day, the root-pressure is of a negative character. Thus, if an actively transpiring plant be cut off near the root, no outflow of water will take place. On the other hand, the stump will energetically draw in water supplied to it; and not until it has become saturated does the force of the root-pressure make itself apparent. In plants growing under natural conditions, the root-pressure is only effective on damp, cool days, or at nights, when the transpiration is greatly diminished. In spring, when the roots are beginning their activity, the conditions are most favourable, the wood is full of water, and the transpiring leaves are not yet unfolded. When the wood is injured at this season "sap" is exuded in drops from the vessels and tracheides.

The so-called BLEEDING from wounds or cut stems is chiefly due to root-pressure, but it is also augmented by the pressure exerted by the living cells of the wood (wood parenchyma, medullary rays). FOR THE LIVING CELLS OF ALL OTHER PARTS OF THE PLANT LIKE THOSE OF THE ROOT ARE UNDER CERTAIN CONDITIONS ABLE TO FORCE OUT FLUID. In addition to an excess of water in the plant the phenomenon may be determined or increased by the stimulus of wounding or by the healing processes; this was shown by MOLISCH for the inflorescences of Palms and in borings made in our native trees. The amount of fluid excreted from the callus tissue in the latter case was small, but was forced out even when the pressure amounted to 9 atmospheres. In *Schizolobium excelsum* Figdor found, in Java, a pressure of 8 atmospheres (24). The outflowing sap often contains, in addition to numerous salts, considerable quantities of organic substances (dissolved albuminous matter, asparagin, acids, and especially carbohydrates). The amount of saccharine matter in the sap of some plants is so great that sugar may be profitably derived from it. The sap of the North American sugar maple, for example, contains ½ per cent of sugar, and a single tree will yield 2-3 kilos. The sap of certain plants is also fermented and used as an intoxicating drink (birch wine, palm wine, pulque, a Mexican beverage made from the sap of *Agave*, etc.). One inflorescence of *Agave* will yield 1000 litres of sap in from four to five months.

The bleeding which takes place on warm, sunny winter days from wounds or borings in trees is not due to root-pressure, but to purely physical causes. It is brought about by the expansion of the air-bubbles in the tracheal elements of the wood, and may be artificially produced at any time in winter by warming a freshly cut piece of wood; when the wood is allowed to cool, the air contracts and the water in contact with the cut surface will be again absorbed.

In some lianes the vessels are so wide that they do not retain the water by capillarity. When such stems are cut drinkable water flows from them in considerable quantity.

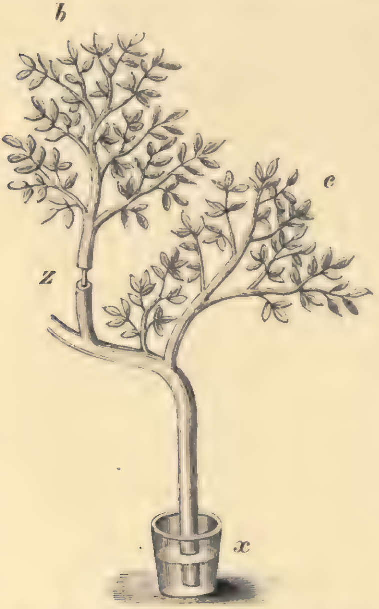


FIG. 188.—HALES' experiment to show the ascent of the sap in the wood. Although the cortex has been entirely removed at *Z*, and the wood alone left, the leaves of the branch *b* remain as fresh as those on the uninjured branch *e*; *x*, vessel containing water. Facsimile of the illustration in HALES' *Vegetable Statics*, 1727.

2. THE COURSE OF THE WATER IN PLANTS.—In living plant-tissues the cells of which require more or less water for their growth and for the maintenance or augmentation of their turgidity, there is a constant transfer of water from one cell to another. This transfer between the adjacent cells takes place much too slowly to equalise the great amount of water lost by evaporation from the foliage of a tall tree. IN ORDER TO TRANSFER THE WATER, QUICKLY AND IN LARGER QUANTITIES, FROM THE ROOTS TO THE LEAVES, PLANTS MAKE USE, NOT OF THE LIVING PARENCHYMA, BUT OF THE WOODY PORTION OF THE VASCULAR BUNDLES. The woody elements which thus conduct the water have no protoplasm.

3. THE TRANSPIRATION CURRENT.—It has long been known that the ascending transpiration current in woody plants flows solely through the wood. It had been observed that plants from which portions of the cortex had been removed, either purposely or acci-

dentally, remained nevertheless perfectly fresh. The adjoining figure, taken from one of the first books in which the vital processes in plants were described (ESSAYS ON VEGETABLE STATICS, by STEPHEN HALES, 1727), shows the method employed in proving this fact experimentally (Fig. 188). At *Z* in the branch *b* all the tissues external to the slender column of wood have been removed. Since the leaves of this branch remain as fresh as those of the branch *c*, it is evident that the transpiration current must pass through the wood and not through the cortical tissues. On the other hand, when a short length of the wood is removed from a stem, without at the same time unduly destroying the continuity of the bark, the leaves above the point of removal will droop as quickly as on a twig cut off from the stem. It has also been shown by experiment that in herbaceous plants the vascular portions of the bundles provide for the conduction of the ascending currents.

As can be demonstrated by spectroscopical analysis, a dilute solution of lithium nitrate taken up by an uninjured plant first ascends in the wood before it passes laterally into the other tissues. By means of the same solution, MACNAB, PFITZER, and SACHS determined the velocity of the movement of the transpiration current, which naturally varies according to the plant and the effect of external conditions upon transpiration ; under favourable circumstances it attains a rate of 1-2 metres an hour. The method of showing the exclusive share of the wood in the conduction of the water, and, also, of determining the maximum velocity of the transpiration current, from observations based on the path and rate of movement of a coloured solution taken up by a plant, is not free from objection, for the colouring matter does not pass through the stem at the same rate as the water in which it is dissolved, but is drawn out and held back by the cells. The employment of coloured solutions will, however, be found instructive for merely showing the course of the transpiration current. The transparent stems of the Balsam, *Impatiens parviflora*, and the white floral leaves of Lilies, Camellias, Mock Orange, etc., in which the coloured vascular system will stand out as a fine network, are especially adapted for such an experiment.

In water plants and succulents, in which little or no transpiration takes place, the xylem is correspondingly feebly developed. In land plants, on the other hand, and especially in trees with abundant foliage, the wood attains a much greater development. All the wood, however, of a large stem does not take part in the task of water-conduction, but only the younger, outer rings. Where there is a distinction between heart- and sap-wood, the heart-wood takes no part in the conduction of the water.

The character of the forces which cause the ascent of the transpiration current is still unexplained. Transpiration itself makes a place for the inflowing water. By the removal of the imbibition water from the cell wall, which is replaced at the expense of the supply contained in the osmotically active cell, force is exerted which causes the water in the adjacent elements of the xylem to move onwards. It is, however, doubtful whether this initial disturbance of the condition of equilibrium is sufficient to effect the raising of the whole mass of water. A sufficient and generally accepted explanation of this much-debated question is still wanting, though progress has been made towards it (25).

It has been already explained that the ROOT-PRESSURE cannot exert such a force during transpiration (p. 201).

OSMOTIC FORCES act too slowly to be of any value, and, moreover, there is no fixed distribution of osmotic substances that would account for such a current.

The transpiration current cannot be due to CAPILLARITY. In the first place, continuous capillaries are entirely wanting in some plants (the Conifers, for example), and in the stems of others they are only present for comparatively short distances. Secondly, the concave menisci in the elements of the wood are not in relation with any level or convex surface of water, in which case alone they could have effect. Thirdly, the height to which liquids can rise by capillary attraction—and it would be less in the vessels and tracheides than in a glass tube—does not approach the height of an ordinary tree; and, finally, the rate of ascent induced by capillarity decreases so greatly with the increasing height of the fluid, that so copious a flow of water as occurs in plants would be impossible.

ATMOSPHERIC PRESSURE has, also, been shown not to be the cause of the transpiration current. In fact the vessels and tracheides of vigorously transpiring plants contain rarefied air between the short columns of water. This is evident from the way in which stems cut under mercury become penetrated by it. But as the watercourses in plants are all completely shut off from the outer atmosphere, the external atmospheric pressure could have no effect. The rarefied air within the plants, moreover, shows no such regularity in its distribution that it could possibly give rise to so continuous a flow of water. Further, as the atmospheric pressure can only sustain the weight of a column of water 10 m. high, while sap rises in *Sequoia* 100 m. high, and in *Eucalyptus* trees of the height of 155 m., the inadequacy of the atmospheric pressure to give rise to such a movement must be admitted.

The supposition that the water ascends in the form of vapour through the cavities of the wood, and is afterwards condensed in the leaves, is untenable, as is at once obvious from a consideration of the anatomical structure of the wood, the interruption of its cavities by short columns of water, and the temperature of the plants themselves. And, moreover, the special task of the transpiration current, to transfer the nutrient salts, could not be accomplished if such were the mode of ascent.

It has also been suggested that all of these processes might be aided by THE CO-OPERATION OF THE LIVING CELLS which are so abundant throughout the wood, and have command of active osmotic forces, to the service of which they could unite a regulative irritability. STRASBURGER's investigations, however, have shown that poisonous solutions, which would at once kill all living protoplasm, can be transported to the summits of the high trees. Thus the supposition that the living elements at least immediately co-operate in the ascent of water is precluded.

Recently JOLY, DIXON, and ASKENASY have endeavoured to explain the transmission of the suction force of transpiration to the most distant root-tip by the fact of the cohesive force of the water. The occurrence of bubbles of air and vapour in the conducting channels, and the fact that movement of the water interferes with the power of its cohesive force to resist a pull are among the objections to this theory, which have, however, been lessened by recent investigations of STEINBRINK (26).

The recent investigations agree, however, in concluding that THE TRANSPIRATION CURRENT ASCENDS IN THE CAVITIES OF THE WOOD THROUGH THE VESSELS AND TRACHEIDES.

4. SUCTION-FORCE OF TRANSPIRING SHOOTS.—A shoot, the cut end of which is placed in water, shows by remaining fresh that it must be able to draw up water to its extreme tips. The force of suction exerted by such a transpiring leafy shoot may be demonstrated, by fitting the cut end in a long glass tube filled with water in such a manner that it shall be air-tight. Thus arranged, the shoot will be able to sustain and raise a column of water 2 metres high. If the lower end of the tube be inserted in mercury, it will be found that even the heavy mercury will be lifted by the transpiring shoot to a considerable height. Vigorous coniferous shoots absorb water through the cut end with a force of suction equal to one atmosphere, and are thus able to raise the mercury to a height equal to the barometric pressure (760 mm.), and owing to the cohesion of the water column even beyond this (920 mm.). The complete exclusion of the external atmosphere is absolutely requisite for the existence of such a suction-force, and this condition is actually fulfilled in the water-courses of plants (27).

The Giving-off of Water.—The requisite amount and proper concentration of the nutrient water supplied by the transpiration current are maintained only by the constant discharge of the accumulating water. This may occur in two ways, either by the evaporation of the water through the cell walls and the stomata in the form of vapour—that is, by transpiration—or less copiously and also less frequently by the actual exudation of drops of water.

1. TRANSPIRATION.—In their outer covering of cork, cuticle, and wax, plants possess a protection from a too rapid loss of water. A pumpkin, with its thick cuticle and outer coating of wax, even after it has been separated from its parent plant for months, suffers no great loss of water. A potato or an apple is similarly protected by a thin layer of cork from loss of water by evaporation. The green organs of plants, on the other hand, which must be able to get rid of the surplus water in order to secure the concentration of the nutrient salts, make little use of such protective coverings. On the contrary, they are provided with special contrivances for promoting evaporation.

The cell walls of all living organs are saturated with water, and, when the cuticle of the epidermis is not too strongly developed, water is constantly evaporated, even from uninjured epidermal cells, in amounts varying with the area of the exposed surfaces. From this point of view, it will be seen that THE FLAT EXPANSION OF FOLIAGE LEAVES RENDERS THEM ADMIRABLY ADAPTED FOR THE WORK OF TRANSPIRATION. Evaporation is also greatly promoted by the numerous STOMATA (AIR-PORES) which perforate the epidermis, and give the air, saturated with watery vapour, an opportunity to escape from the intercellular spaces. Although the stomata are so small (0·0006 mm. and less) that neither dust nor water can pass through them into the plant, they are usually present in such enormous numbers (p. 104) and so suitably distributed that their united action compensates for their minuteness. When it is taken into consideration that a medium-sized cabbage leaf (*Brassica oleracea*) is provided with about eleven million, and a Sunflower leaf with about thirteen million air-pores, it is possible to estimate how greatly evaporation must be promoted by diffusion through these fine sieve-like perforations of the epidermis (cf. p. 221).

The stomata also afford plants a means of REGULATING EVAPORATION. The pores, which are the mouths of intercellular spaces, are surrounded by GUARD-CELLS (p. 103). As the term guard-cell suggests, these cells have the power of closing the pore. THE CLOSING AND OPENING OF THE STOMATA ARE ACCOMPLISHED THROUGH CHANGES IN THE TURGIDITY OF THE GUARD-CELLS OR OF THE ADJOINING EPIDERMAL CELLS. In consequence of their peculiar wall thickenings, elasticity, and lateral attachment, a change of turgidity affects the size and shape of the guard-cells in such a way that, on diminished turgidity, they become flatter and close the air-passage, while an increase of turgidity has the contrary effect and opens the pore (Fig. 189).

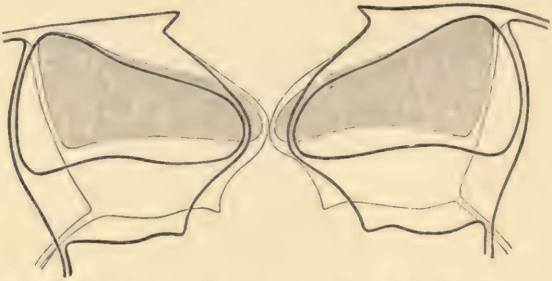


FIG. 189.—Stoma of *Helleborus sp.* in transverse section. The darker lines show the shape assumed by the guard-cells when the stoma is open, the lighter lines when the stoma is closed. (After SCHWENDENER.) The cavities of the guard-cells with the stoma closed are shaded, and are distinctly smaller than when the stoma is open.

In many plants the so-called subsidiary cells (p. 104) participate in various ways and degrees in these processes, depending upon the special structure of the whole apparatus. The opening and closing of the stomata may follow either external or internal influences; but such stimuli affect different plants in different manners. Generally speaking, the stomata begin to close on the diminution of the water-supply, even before this is indicated by wilting; they open, on the other hand, when active transpiration is advantageous (in light, in moist air, etc.). The quantity and quality of the substances held in solution in the nutrient water and the nature of the surrounding gases react upon the stomata. The size of their opening is decreased, and the quantity of water evaporated is therefore lessened when more than the usual amount of nutrient salts is present in the transpiration current; as in that case, if through continued evaporation the nutrient water should become too concentrated, it might act injuriously upon the plant. In marsh and water plants the stomata react less promptly than in land plants ([28]).

It has already been pointed out, in describing the morphology of the stomata, that they are chiefly to be found on the surfaces of the leaves. THE LEAVES ARE ACCORDINGLY TO BE CONSIDERED AS SPECIAL ORGANS OF TRANSPIRATION (and assimilation, p. 214). This is also evident from the extraordinarily minute branching and subdivision of the vascular bundles in the blade of the leaf. The adjoining illustration (Fig. 190), showing the nervature or distribution of the vascular bundles in a *Crataegus* leaf, will convey some idea of the extensive branching which the bundles of a leaf undergo, especially when it is taken into consideration that only the macroscopic and none of the finer microscopic branchings are represented in the figure. By means of this conducting system, a copious supply of nutrient water can be delivered directly from the roots to every square millimetre of the leaf. There is, however, a special reason why the leaves are so abundantly supplied. They are the actual laboratories of plants, in which, out of the carbonic acid of the atmosphere and the water, and nutrient salts of the soil, the organic building material of the plant-body is produced. For this reason it is in the leaves that the broad expansions of tissue for the special promotion of transpiration are found. The amount of water actually evaporated from the leaf surfaces in the performance of their vital functions is surprising. For instance, a strong Sunflower plant, of about the height of a man, evaporates in a warm day over a litre of water. It has been estimated that an acre of cabbage plants will

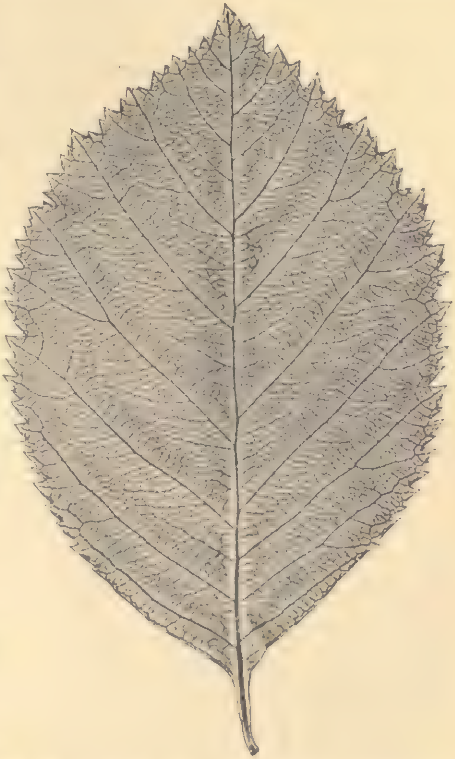


FIG. 190.—Course of the vascular bundles (venation) in a leaf of *Crataegus*. (From a photograph; natural size.)

give off two million litres of water in four months, and an acre of hops three to four millions. For a Birch tree with about 200,000 leaves and standing perfectly free, VON HOHNEL estimated that 500 litres of water would be lost by evaporation on a hot dry day ; on an average the amount would be 60-70 litres. A hectare of Beech wood gives off on the average about 30,000 litres daily (29).

It has been calculated that during the period of vegetation the Beech requires 75 litres and the Pine only 7 litres for every 100 grammes of leaf substance. According to DIETRICH, for every gramme of dry, solid matter produced, on the average, 250-400 grammes of water are evaporated.

EXPERIMENTAL DEMONSTRATION OF TRANSPIRATION.—The evaporation from plants, although imperceptible to direct observation, may be easily demonstrated, and its amount determined by the help of a few simple appliances. One method of doing this is to weigh a plant before and after a period of vigorous evaporation, and thus determine the amount of water actually lost. Or, if the water evaporated by a plant placed under an air-tight bell-jar be absorbed by calcium chloride or concentrated sulphuric acid, it will only be necessary to determine the increase in weight of the absorbing substance to estimate the amount of water given off by evaporation. The amount of water taken up by a plant may also be shown by so arranging the experiment that the water passes in through a narrow tube, as then even a small consumption of water will be quickly indicated by the rapid change of the water-level, which will be the more rapid the smaller the bore of the tube. An apparatus of this kind is called a potetometer, and by its means the amount of water taken up by a transpiring branch may be determined.

The important part taken by the stomata in the process of transpiration may be easily shown, according to STAHL, by means of the cobalt reaction, or the change in colour of dark-blue dry cobalt chloride to light rose upon absorption of water. In making this experiment a leaf placed between strips of paper which have been previously saturated with this cobalt salt and then thoroughly dried, is laid between glass plates. The paper on the side of the leaf most abundantly supplied with stomata will then first change its colour, and that too the more rapidly the more widely open are the stomata. The cobalt reaction, as also the iron and palladium chloride reaction used by MERGET, may be used to determine variations in the width of the stomatal openings. FR. DARWIN used a delicate hygrometer for this purpose in order to follow continuously the variations in width of the opening.

By the dimming of a film of collodion through which all the microscopic detail of the leaf surface could be seen, BUSCALIONI and POLLACCI were able to prove that a slight general transpiration in addition to that through the stomata takes place (30).

It is evident from these and similar experiments that more water is evaporated in a given time from some plants than from others. These variations are due to differences in the area of the evaporating surfaces and to structural peculiarities (the number and size of the stomata, presence of a cuticle, cork, or hairy covering, etc.). But even in the same shoot transpiration is not always uniform. This is attributable to the fact that, both from internal and external causes, not only the size of the openings of the stomata varies, but also that transpiration, just as evaporation from a surface of water, is dependent upon external conditions. Heat, as well as the dryness and motion of the air, increases transpiration for purely physical reasons ; while light, for physiological reasons, also promotes it. From both physical and physiological causes, transpiration is more vigorous during the day than night. Plants like *Impatiens parviflora*, which droop on warm days, become fresh again at the first approach of night.

2. EXUDATION OF WATER.—The discharge of water in a liquid state by direct exudation is not of so frequent occurrence as its loss by evaporation in the form of vapour. Early in the morning, after a warm, damp but rainless night, drops of water may be observed on the tips and margins of the leaves of many of the plants of a meadow or garden. These drops gradually increase in size until they finally fall off and are again replaced by smaller drops. These are not dew-drops, although they are often mistaken for them; on the contrary, these drops of water exude from the leaves themselves. They are discharged near the apex of the leaves of the Indian Corn, but in the case of *Alchemilla* from every leaf-tooth, and of the Nasturtium from the ends of the seven main nerves (Fig. 191). The drops disappear as the sun becomes higher and the air warmer and relatively drier, but can be induced artificially if a glass bell-jar be placed over the plant, or the evaporation in any way diminished. When the plant becomes overcharged with water through the activity of the roots, it is discharged in drops. These are pressed out of special water-stomata (p. 104) or in other cases through the ordinary stomata, or from clefts in the epidermis.

MARINE BIOLOGICAL LABORATORY
WOODS HOLE
LIBRARY
MASS.

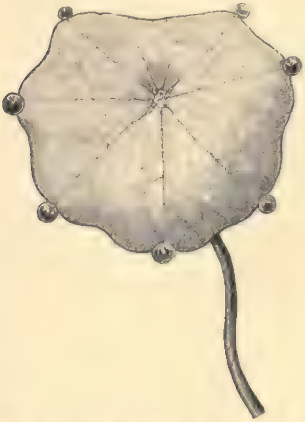


FIG. 191.—Exudation of drops of water from a leaf of *Tropaeolum majus*.

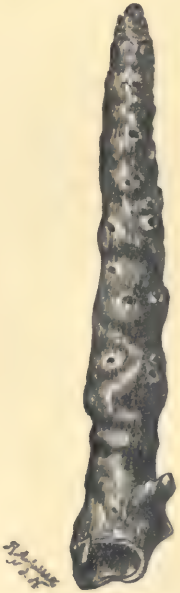


FIG. 192.—Resinous covering of the stem of a desert plant (*Sarcocaulon*). (From SCHIMPER'S *Plant-Geography*.)

Sometimes they are secreted by specially constructed hairs, and in *Datura* the water is excreted through the walls of the ordinary epidermal cells.

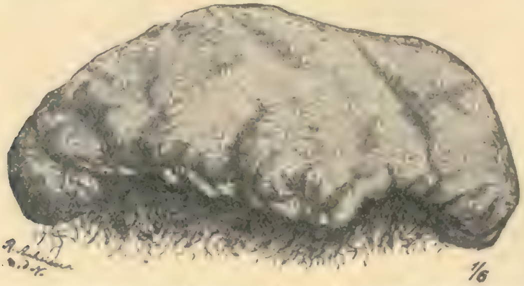

R. Anheisser n. d. N.
1/6

FIG. 193.—*Raoulia mammillaris* from New Zealand, showing the cushion-like shape of the individual plant. (From SCHIMPER'S *Plant-Geography*.)

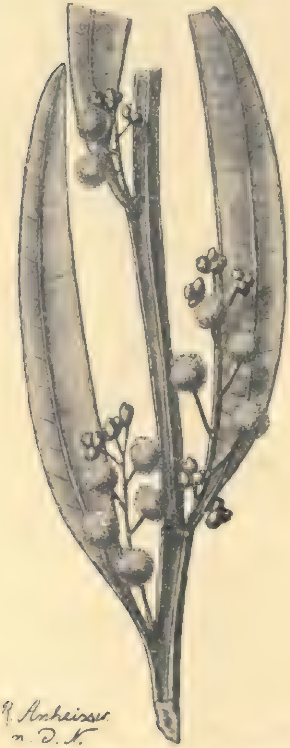

R. Anheisser n. d. N.

FIG. 194.—*Acacia marginata*, an Australian sclerophyllous plant, showing phyllodes. (From SCHIMPER'S *Plant-Geography*.)

It is possible to cause similar exudation of water in drops by forcibly injecting water into a cut shoot.

Such exudations of water are particularly apparent on many Aroids, and drops of water may often be seen to fall within short intervals, from the tips of the large leaves. From the leaves of *Colocasia nymphaefolia* the exuded drops of water are even discharged a short distance, and 190 drops may fall in a minute from a single leaf, while $\frac{1}{10}$ litre may be secreted in the course of a night. In *Spathodea*, a tropical member of the Bignoniaceae, and some other plants, the space enclosed by the calyx, in which the young floral organs are developed, is filled with water. Again, in unicellular plants, especially some Moulds, the copious exudation of water is very evident. The water in this case is pressed directly through the cell walls, and in some cases also, as is the case in water plants, through the easily permeable cuticle (31).

The organs for the discharge of water, which HABERLANDT has collectively termed hydathodes (p. 108), in some instances, actively press out the water; or, on the other hand, they may simply allow it to filter through them when the internal pressure has attained a certain strength, and has caused the water to fill the intercellular spaces. Hydathodes are mostly found on young organs and are early developed on them.

Since the excretion of water in the liquid form can occur when the conditions are unfavourable to transpiration (*Lathraea*) it may in a sense take the place of transpiration in maintaining the current from the water-absorbing organs. Its physiological significance is not, however, the same as transpiration, since the expressed water always contains salts, and sometimes also organic substances in solution. In fact the quantity of salts in water thus exuded is often so abundant that after evaporation a slight incrustation is formed on the leaves (the lime-scales on the leaves of Saxifrages) (³²).

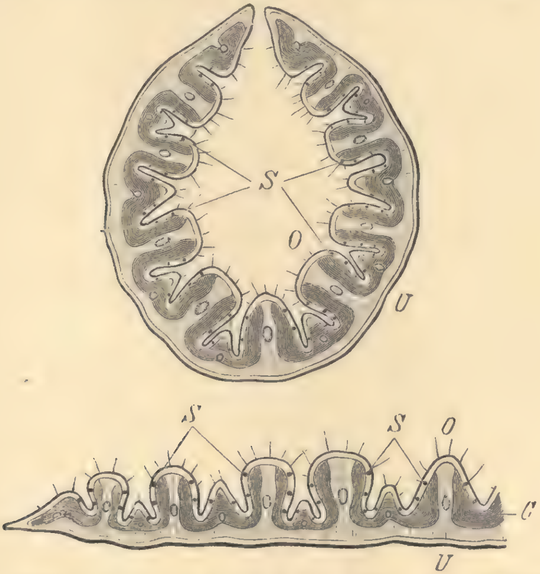


FIG. 195.—Transverse sections of the leaf of *Stipa capillata*. The leaf above in the closed state, the half leaf below expanded. *U*, lower surface, without stomata; *O*, upper surface with stomata (*S*); *C*, chlorophyllous mesophyll. (× 30. After KERNER VON MARILAUN.)

In some instances, also, the substances in solution in the water are exuded with a purpose, as in the case of the secretions of the NECTARIES, of the DIGESTIVE GLANDS of insectivorous plants, and of the discharge of the viscid STIGMATIC FLUID. The excreted substances in these instances exert an osmotic attraction on the water in the cells of the plant; this distinguishes such cases from excretion dependent simply on the internal pressure. The substances excreted by some desert plants (*Reaumuria*, *Tamarix*) are so strongly hygroscopic that the leaves remain covered with numerous drops of liquid even in the dry air and under the arid conditions natural to the plants. The superfluous water is discharged by a few plants, the Pumpkin, for example, into the cavities of their stems and leaf-stalks, and is again absorbed from these reservoirs when needed (33).

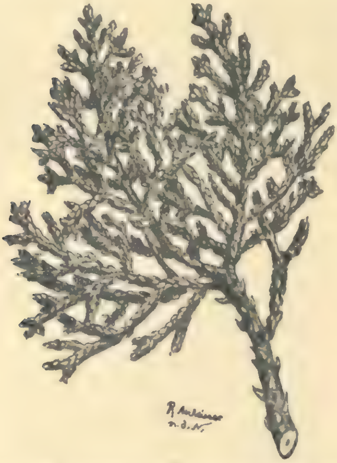


Fig. 196.—*Veronica cupressoides*, with the habit of a Cypress, from New Zealand. (From Schimper's *Plant-Geography*.)

Special Contrivances for regulating the Water-supply.—Almost all the higher plants possess, in the power to close their stomata, a special means of checking transpiration during a temporary insufficiency of the water-supply. In districts subject to droughts of weeks' or months' duration, only such plants can flourish as are able either to withstand a complete drying up without injury (p. 195), or to exist for a long time on a scanty supply of water (xerophytes). This last case is only rendered possible by the extreme reduction of transpiration, or by the formation of organs in which, in times of a superfluity of water, it may be retained for later use.

Such protection against excessive transpiration is afforded by the formation of cork or cuticular coverings and in exceptional cases coverings of resin (Fig. 192), by the reduction in the number and size of the stomata, their occurrence in cavities or depressions, and the more or less complete filling of the opening by waxy substances. The rolling up of the leaves, the stomatiferous surface being on the concave side, as well as the development of thick growths of hair, or of a covering of star-shaped or scaly hairs, and the assumption of a vertical position to avoid the full rays of the sun, are also measures frequently adopted to lessen transpiration. The most efficient protection, however, from too great a loss of water by transpiration is undoubtedly obtained by the reduction of the transpiring surfaces, either through a diminution in the size of the leaves or through their complete disappearance. The same result may be obtained by the crowding of the branches of the plant to form a dense cushion (Fig. 193).

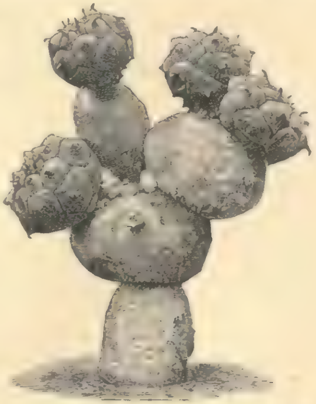


Fig. 197.—*Euphorbia globosa*. The reduced leaves may be seen on the upper globose shoots.

The upright position of the leaves, or the substitution of expanded, perpendicularly directed leaf-stalks for the leaves (Phyllodes), particularly characterises the flora of Australia (Fig. 194). A clothing of hair, on the other hand, protects the leaves of some South African Proteaceae (*e.g. Leucadendron argenteum*). Some of the Gramineae (*Stipa capillata*, *Festuca alpestris*, *Sesleria tenuifolia*, *S. punctoria*, etc.) roll or fold their leaf-blades, in times of drought, by means of special hinge-like devices, into narrow tubes, the protected inner surface being formed by the side bearing the stomata. Reduction of the leaves is illustrated by the desert forms of *Genista* and *Sarothamnus*, and by the Cypress-like Conifers. The New Zealand *Veronica*, shown in Fig. 196, closely resembles these in habit. A complete disappearance of the whole leaf surface takes place in most *Cacti*, in which also the stems become swollen and converted into water-reservoirs. A similar development of succulent swollen stems frequently occurs in the Euphorbiaceae (Fig. 197), in the Compositae (*Kleinia articulata*), Asclepiadaceae, and other plant families found in arid regions. It has been estimated (34) that the amount of water evaporated by a Melon-Cactus is reduced by its succulent development to $\frac{1}{6000}$ of that given off by an equally heavy climbing plant (*Aristolochia*). Instead of the stem the leaves themselves may become succulent, as in the House-leek and other species of *Sempervivum*, also in many species of *Sedum*, *Aloe*, and *Agave*. Both stem and leaves are equally succulent in many species of *Mesembryanthemum*. In other plants, the parenchyma of their stem tubers (epiphytic Orchids) or of their thickened roots (Oxalideae) serve as water-reservoirs. Epiphytic Bromeliaceae catch the rain-water in reservoirs formed by their closely approximated leaves, and then eagerly take it up through the scaly hairs which cover the leaf surfaces, as in species of *Tillandsia*. Again, many epiphytic Orchids and Aroids collect the rain-water in a swollen sheath developed from the epidermis of the aerial root (velamen radicum, p. 109). In the case of other epiphytic Orchids, Aroids, and Ferns (*Asplenium Nidus*, for instance), the humus and other material caught in receptacles formed by the leaves or aerial roots act like a sponge in taking up and retaining water, while the absorptive roots penetrate into these moist, compost-like masses and absorb both water and nutrient substances. Many species of *Frullania* (a Liverwort common on Beech trees) possess, on the other hand, special water-sacs on the under side of their thallus (Fig. 386). A particularly remarkable contrivance for maintaining a constant supply of water is exhibited by the epiphytic *Dischidia Rafflesiana*, a number of whose leaves form a deep but small-mouthed urn, into which the roots grow. It would seem at first sight unnecessary that plants like the Mangrove tree, which stand with their roots entirely in water, should require protection against too rapid transpiration ; but, as this tree grows in salt or brackish water, it is necessary, as in other halophytes (Fig. 184) to reduce the amount of water absorbed, in order to prevent a too great accumulation of salt in the tissues.

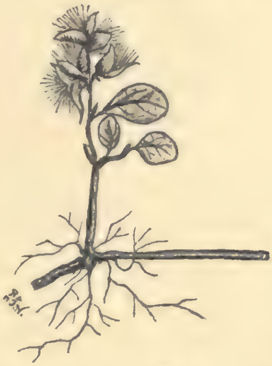


FIG. 198.—*Salix polaris*. Full grown and bearing fruits. (Nat. size ; from SCHIMPER'S *Plant-Geography*.)

In high latitudes, where the soil remains frozen for months at a time, rendering the absorption of water by the plant difficult, arrangements similar to those found in desert plants are present to diminish transpiration. The dwarf habit which is so frequently characteristic of the alpine and arctic plants (Fig. 198) is as much an expression of this limitation of the transpiration as of the generally unfavourable conditions of existence (35).

The Absorption of Carbon (Assimilation)

In any attempt to distinguish the relative importance of substances utilised in plant nutrition, carbon undoubtedly ranks first. Every organic substance contains carbon, and there is no other element which could supply or take part in the formation of so many or such a variety of substances, in living organisms as in the chemical laboratory. Organic chemistry, in short, is merely the chemistry of carbon compounds. Living beings which are composed of organic substances owe the possibility of their existence primarily to the properties of carbon.

It requires no chemical analysis to realise that plants actually contain carbon, although in an imperceptible form. Every burning splinter of a match shows, by its charring, the presence of this element. An examination of a piece of charcoal in which the finest structure of the wood is still distinguishable, shows how abundant is the carbon and how uniformly distributed. Estimated by weight, the carbon will be found to make up about half the dry weight (when freed from water) of the plant. The great quantities of coal in the deeper strata of rocks are the remains of ancient plants; both in peat and in some cases in coal the macroscopic and microscopic structure gives proof of this origin.

Whence do plants derive this carbon? The "humus" theory, accepted for a long time, assumed that the humus of the soil was the source of all the supply; and that carbon, like all the other nutrient substances, was taken up by the roots. That plants grown in pure sand free from humus, or in a water-culture, increase in dry substance, and consequently in carbon, clearly demonstrates the falsity of this theory. The carbon of plants must therefore be derived from other sources; and, in fact, the carbon in humus is, on the contrary, due to previous vegetable decomposition. The discovery made at the end of the eighteenth and the beginning of the nineteenth century, that THE CARBON OF PLANTS IS DERIVED FROM THE CARBONIC ACID OF THE ATMOSPHERE, and is taken up by the action of the green leaves, is associated with the names of INGENHOUSS, SENEBIER, THEO. DE SAUSSURE, and SACHS. This discovery is one of the most important in the progress of the natural sciences. It was by no means easy to prove that the invisible gaseous exchange between a plant and the atmosphere constitutes the chief source of nourishment; and it required the courage of a firm conviction to derive the thousands of pounds of carbon accumulated in the trees of a forest, from the small proportion (0·03 per cent) of carbon dioxide contained in the atmosphere.

The amount of carbonic acid gas contained in the air varies at different times and places. H. BROWN found that in 10,000 litres of air it was 2·7-2·9 litres in July, 3·0-3·6 litres in the winter; close to the ground 12-13 litres were present in the same volume. The average amount is about 3⅓-3½ litres in 10,000 litres of the atmosphere. This weighs about 7 grammes, of which $\frac{8}{11}$ is oxygen, and only $\frac{3}{11}$ carbon. Only 2 grammes of carbon are thus contained in the 10,000 litres of air. In order therefore for a single tree having a dry weight of 5000 kilos to acquire its 2,500,000 grammes of carbon, it must deprive 12 million cubic metres of air of their carbonic acid. From the consideration of these figures, it is not strange that the discovery of INGENHOUSS was unwillingly accepted, and afterwards rejected and forgotten. LIEBIG was the first in Germany to again call attention to this discovery, which to-day is accepted without question. The immensity of the numbers just cited are not so appalling when one considers that, in spite of the small percentage of carbonic acid in the atmosphere, the actual supply of this gas is estimated at about 3000 billion kilos, in which are held 800 billion kilos of carbon. This amount would be sufficient for the vegetation of the entire earth for a long time, even if the air were not continually receiving new supplies of carbonic acid through the respiration and decomposition of organisms, through the combustion of wood and coal, and through volcanic activity. An adult will exhale daily about 900 grammes CO_2 (245 grammes C). The 1400 million human beings in the world would thus give back to the air 1200 million kilos of CO_2 (340 million kilos C). The CO_2 discharged into the air from all the chimneys on the earth is an enormous amount. CREDNER calculated that 460,000,000,000 kilos of coal are burnt annually, yielding to the atmosphere about 1,265,000 million kilogrammes of carbonic acid gas. These sources of CO_2 are, according to Beyerinck, insignificant compared with the enormous amounts produced by the bacteria of the soil in putrefactive processes. The whole carbon supply of the atmosphere is at the disposal of plants, since the CO_2 becomes uniformly distributed by constant diffusion.

Not all plants, nor indeed all parts of a plant, are thus able to abstract the carbon from the carbonic acid of the air. Only such organs as are coloured green by chlorophyll are capable of exercising this function, for the chlorophyll bodies themselves are the laboratories in which this chemical process, so important for the whole living world, is carried on. From these laboratories is derived the whole of the carbon which composes the organic substance of all living things, plants as well as animals. Animals are unable to derive this most essential element of their bodies from inorganic sources. They can only take it up in organic substances, which have been previously formed in plants. Such plants, also, as are without chlorophyll, as, for example, the Fungi and some of the higher parasitic plants, are dependent for their nutrition upon organic substances previously formed by the chlorophyll bodies of other plants.

Roots and other organs unprovided with chlorophyll, and also the colourless protoplasm in the green cells themselves, are similarly dependent upon the activity of the chloroplasts.

The derivation of carbon from carbonic acid and its conversion into organic substances is termed ASSIMILATION. In its broadest sense, and especially in the animal kingdom, the word assimilation is used for all nutritive processes by which the nourishment is built up into the substance of an organism. But in Botany the meaning of the term has gradually been restricted, and now by assimilation the assimilation of carbon by means of the chlorophyll granules is specially understood. Moreover, all the further synthetic processes of assimilation are dependent upon carbon assimilation.

The chlorophyll bodies, however, can only produce organic substances from carbonic acid and water by help of the vibrations of light (PHOTOSYNTHESIS). The chlorophyll apparatus is unable to assimilate in darkness, although all the other requirements are present for active assimilation. Given a source of illumination, either natural or artificial, assimilation commences, and, within certain limits, increases in proportion to the intensity of the effective rays. Unfavourable conditions, such as cold, or the presence of poisonous substances, may inhibit the action of the chlorophyll apparatus.

The vibrations of the ether perceptible as light supply the energy for the decomposition of carbonic acid and the production of carbon, just as other vibrations, in the form of heat, supply the energy requisite for the working of a steam-engine. A considerable amount of work has to be done in the assimilation of carbon, and on the potential energy thus stored up the vital processes are mainly dependent. Even the force exerted by the steam engine can be referred to the work of assimilation which was performed by the plants whose remains are burnt in the furnace. For in the process of combustion the organic material is oxidised producing carbon dioxide, and the energy which was originally needed to produce the substance of the plants from carbon dioxide is set free.

Not all light vibrations are equally capable of arousing the assimilatory activity. Just as the rays of different refrangibility differ in their action, both upon the eye and the photographic plate, so they have a different effect upon assimilation. It would be natural to suppose that the chemically active rays, the blue and violet, which decompose silver salts and other chemical compounds, would also be the most effective in promoting the assimilatory activity of the chlorophyll bodies. Exactly the contrary, however, has been shown to be the case. The highly refractive chemical rays have little or no effect on assimilation; the red, orange, and yellow rays, that is, the so-called illuminating rays of the spectrum, are on the contrary the most active ([36]).

In the red-leaved varieties of green plants, such as the Purple Beech and Red Cabbage, the chlorophyll is developed in the same manner as in the green parent species, but it is hidden from view by a red colouring matter in the epidermis or in deeper-lying cells. In the Red Algae on the other hand the chromatophores themselves have a red colour; after death this becomes free as a bluish-red pigment (phycocyan) leaving the chloroplasts green. The Brown Algae and the Diatomaceae have a brown modification of chlorophyll (phaeophyll) which after death changes into chlorophyll.

In the blue-green freshwater Algae, and also in the Brown and Red Seaweeds, the maximum assimilation takes place, according to ENGELMANN, in another part of the spectrum than it does in the case of green plants. The assimilation in these Algae seems indeed to be carried on in the part of the spectrum, the colour of which is complementary to their own. The pigments associated with the chlorophyll thus appear to act in the same way as the sensibilisators on the photographic plate ; they attract light of a different wave length to co-operate in the chemical process. All the rays of the mixed white light are usually at the disposal of plants growing freely in the open air ; only the Seaweeds found in deep water (at the most but 400 m. below the surface) grow in a prevailing blue light, while the deeper-lying tissues of land plants live in red light, as this penetrates farther into the parenchymatous tissues (37).

In studying the effect of different kinds of light upon assimilation, it is customary either to use the separate colours of the solar spectrum, or to imitate them by means of coloured glass or coloured solutions. For such experiments it will be found convenient to make use of double-walled bell-jars filled with a solution of bichromate of potassium or of ammoniacal copper oxides. Plants grown under jars filled with the first solution, which allows only the red, orange, and yellow rays to pass through, assimilate almost as actively as in white light. Under the jars containing the second solution, which readily permits the passage of the chemically active rays, assimilation is much less active.

But little is known with regard to the processes carried on in green cells during assimilation, and it is still by no means clear what part the green chlorophyll pigment performs. The pigment which may be extracted from the protoplasm of the chlorophyll bodies makes up only a small part of their substance (about 0·1 per cent.), and gives no reaction from which its operations may be inferred. The light absorbed by the chlorophyll pigment also stands in no recognisable relation to the requirements of assimilation, for the assimilation is not proportional to the intensity of the absorption of the different rays. The proportion of the energy, passing through the leaf in the form of light, utilised in assimilation is, according to the thermo-electric measurements of DETLEFSEN, only 1 per cent ; according to the calculations of H. BROWN, ½ per cent in sunlight, and over 2 per cent in diffuse light (38). It has not as yet been determined what part the mineral constituents of the transpiration current take in the process. On the other hand, the protoplasmic body of the chloroplasts cannot assimilate when the green pigment is not present ; that is, when, from any cause, the corpuscles are prevented from turning green. As the existence of the green pigment is dependent upon the presence of oxygen, of iron, of carbohydrates and other food substances, upon a proper temperature, and, with few exceptions (Ferns, Conifers, cotyledons of Sycamore, lower Algae in culture solutions), upon the action of light, its formation in the chlorophyll bodies may be prevented by depriving them of the requisites for its development. The chromatophores will then remain yellow (in leaves) or white (in stems).

Within recent years it has, indeed, been determined that certain nitrifying bacteria have the power of forming a small amount of organic substances from carbonates, carbonic acid, and ammonia. The process by which the organic carbon compound is derived must, however, be altogether different from that of green plants, as the bacteria contain no chlorophyll, and their nutritive activity is in no way dependent upon the light. The necessary energy is here obtained not from photosynthesis but from the oxidation of ammonia into nitrous acid, and this into nitric acid (chemosynthesis). The formation of organic substance in the sulphur bacteria and especially in the so-called purple bacteria is also insufficiently understood, but photosynthesis appears to play a part in it.

As a result of the chemical processes involved in the decomposing activity of assimilation, only the special end-product and one bye-product are at present known. SACHS discovered that the organic compound, first to be detected as the special ultimate product of assimilation in the higher plants, is a CARBOHYDRATE, which may either remain in solution, or in the form of STARCH GRAINS may become microscopically visible at the points of its formation. In a number of plants (*e.g.* the Algae) the first visible product is often not starch but a fatty oil, protein, or some other secondary product.

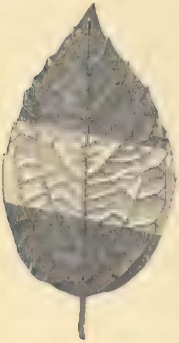


FIG. 199.—A leaf showing the iodine reaction. Part of an assimilating leaf was covered with a strip of tinfoil. Afterwards, when treated with a solution of iodine, the part of the leaf darkened by the overlying tinfoil, having formed no starch, gave no colour reaction. (¾ nat. size.)

A short time after assimilation begins, in sunshine, sometimes within five minutes, minute starch grains appear in the chloroplasts. These grains gradually enlarge until, finally, they may greatly exceed the original size of the chloroplasts. Should, however, the assimilation cease, which it regularly does at night, then the starch grains are dissolved and as soluble carbohydrates (glucose, etc.) pass out of the cell. In some plants (many Monocotyledons) there is no starch formed in the chloroplasts, but the products of assimilation pass in a dissolved state directly into the cellsap. In exceptional cases, however, starch is also formed where there is a surplus of glucose, sugar, and other substances, as, for example, in the guard cells of the stomata of Monocotyledons, and in the coloured plastids of flowers and fruits. In other cases also only a fraction of the product of assimilation appears as starch (in *Helianthus*, for example, only $\frac{1}{6}$) while the carbohydrates formed in the first place (soluble hexoses, especially dextrose $C_6H_{12}O_6$) are in part transformed into di- and poly-saccharides. In a chemical sense the process of assimilation is thus an asymmetrical one.

The formation of starch may be shown to be a direct result of assimilation, by means of the "iodine reaction" and without the aid of a microscope. If a leaf cut from a plant previously kept in the dark until the starch already formed in the leaves has been removed in a soluble form, be treated with a solution of iodine after being first decolorised in hot alcohol, it will in a short time assume a yellowish-brown colour, while a leaf vigorously assimilating in the light will, with the same treatment, take a blue-black colour owing to the starch abundantly present in the cells. In Fig. 199 the result of the iodine reaction is shown on a leaf, part of which had been covered with a strip of dark paper or tinfoil. The cells darkened by the overlying paper or foil formed no starch, while those exposed to the light are shown by the iodine reaction to be full of it. A green leaf kept in air devoid of carbonic acid, although fully exposed to the light, will similarly form no starch.

The bye-product arising from the assimilatory process is PURE OXYGEN. The volume of oxygen thus set free is nearly equal to (in most cases it somewhat exceeds) the volume of carbonic acid taken in. If plants assimilate in a known quantity of air containing carbonic acid gas, its volume will therefore remain nearly the same. The chemical process of assimilation resulting in the decomposition of the carbonic acid may be thus expressed:

$$6CO_2 + 6H_2O = \underset{\text{(Glucose).}}{C_6H_{12}O_6} + 6O_2$$

From this chemical equation(39) it is evident that the ELEMENTS OF WATER ARE REQUISITE FOR THE PROCESS OF ASSIMILATION (p. 189). In the transformation of the mono-saccharides into poly-saccharides (starch, cellulose) which afterwards takes place, small amounts of water are again liberated.

The oxygen given off by green plants, although not perceptible when they are growing in the open air, becomes apparent in the case of water plants. It was indeed through the evolution of bubbles of oxygen from water plants that INGENHOUSS first had his attention called to the assimilatory activity of leaves. To see this process, it is only necessary to place a cut stem of a water plant in a vessel of water exposed to the sunshine, when a continuous series of small bubbles of gas will at once be seen to escape from the intercellular passages intersected by the cut. The gas thus evolved may be collected with little trouble (Fig. 200), and will be found to be chiefly

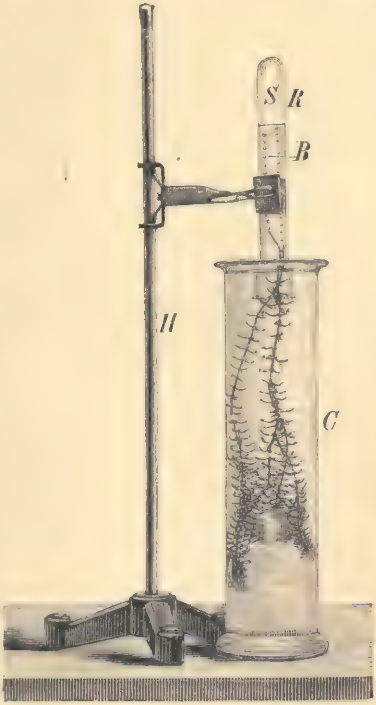


FIG. 200.—Evolution of oxygen from assimilating plants. In the glass cylinder *C*, filled with water, are placed shoots of *Elodea canadensis*; the freshly cut ends of the shoots are introduced into the test-tube *R*, which is also full of water. The gas-bubbles *B*, rising from the cut surfaces, collect at *S*. *H*, stand to support the test-tube.

oxygen, containing, however, under such simple conditions of experiment, traces of other gases derived by diffusion from the plant and the water. As water absorbs much less oxygen than carbonic acid (at a temperature of 14° C. 100 vols. of water will dissolve only 3 vols. of oxygen, but 100 vols. of carbonic acid), the escaping bubbles of oxygen become visible; whereas the flow of the carbonic acid dissolved in the water to the assimilating plant is imperceptible.

Artificially conducting carbonic acid through the water increases, to a certain degree, the evolution of oxygen, and thus the assimilatory activity. Similarly an artificial increase of carbonic acid in the air is followed by increased assimilation. According to KREUSLER assimilation in sunshine attains its maximum in air containing about 10 per cent of carbonic acid; with a higher percentage it begins to decrease. If the amount of carbonic acid gas be increased three hundred times (from 0·03 per cent to 10 per cent in the atmosphere), the formation of starch is only increased 4-8 times, while an increase of the CO_2 to six times the normal proportion results, according to H. BROWN, in the formation of six times as much starch. A longer exposure to an atmosphere rich in CO_2 does not have a favourable influence on the health of the plant; it takes on abnormal modes of growth, loses the power of flowering, and thus makes it evident that it is suited to live in air with the ordinary proportion of CO_2. This may be termed the "harmonic" optimum (40).

Like other vital activities of the plant assimilation is dependent upon the temperature, and at lower grades of temperature is not so great as the available light and carbon dioxide would permit. In bright, warm weather, on the other hand, the small amount of CO_2 in the atmosphere becomes the limiting factor.

Carbon monoxide (CO) cannot be utilised by green plants; it cannot take the place of the carbon dioxide, and is poisonous to plants, though less so than to animals.

Under the same external conditions, the assimilatory activity of different plants may vary from internal causes. In the same time and with an equal leaf surface, one plant will form more, and another less carbohydrate. In this sense, it is customary to speak of a "specific energy of assimilation," which is partly due to the different number and size of the chloroplasts, as well as to a difference in the structure of the leaves, but, without doubt, has also its cause in the greater or less intensity of the assimilatory process itself.

As examples of medium assimilatory activity, the leaves of the Sunflower and Pumpkin may be cited. Under conditions favourable for assimilation, the leaves of these plants, according to SACHS, form in a summer day of fifteen hours about 25 grammes starch per square metre, while *Catalpa*, according to BROWN and ESCOMBE, forms about 3 grammes per hour and square metre of surface. (The carbon for the formation of the starch was supplied in the first cited example from 50 cubic metres of air. A room of 120 cubic metres would accordingly contain enough carbonic acid for 60 grammes of starch.) From these figures a faint conception may be gained of the enormous activity of the assimilatory processes, of the vegetation of the surface of the earth. The German wheat harvest for 1900 represented about 23,000 million kilos of assimilated substance.

The Mechanism of Gaseous Exchange

The gaseous exchange between one of the lower plants (or a submerged Phanerogam) and the surrounding medium is carried on by diffusion through the whole surface of the plant. In a more highly organised plant the exchange takes place by means of the stomata. The escape of aqueous vapour and the entrance and escape of carbonic acid gas and oxygen in the processes of assimilation and respiration (p. 244) alike take place almost entirely through these openings. But in spite of their enormous number, the total area of the stomatal apertures is only about 1 per cent or little more of the whole surface area, for each individual opening is very small (about 0·0001 sq. mm. in *Helianthus*). BROWN and ESCOMBE have, however, shown that the minuteness of the openings, combined with the peculiar distribution of the stomata, results in a greatly accelerated rate of diffusion. Diffusion through a number of fine apertures is much greater than through a single aperture of the same total area. When the small openings are placed about ten times their diameter apart the diffusion is nearly as rapid as when no separating wall is present. The distribution of the stomata in the epidermis very nearly meets these requirements. For example, a square metre of the surface of a *Catalpa* leaf absorbs about two-thirds the amount of carbonic acid gas taken up in an equal time by the same area of potash solution freely exposed to the air (41).

The Utilisation of the Products of Assimilation

The Formation of Albuminous Substances.—The chlorophyll bodies supply plants with organic nourishment in the form of a carbohydrate. Although the greater part of the organic plant substance consists only of carbohydrates, as, for example, the whole framework of cell walls, yet the living, and consequently the most important component of the plant-body, the protoplasm, is composed of albuminous substances. These albuminous substances have a composition altogether different from that of the carbohydrates. In addition to carbon, oxygen, and hydrogen, they also contain nitrogen, sulphur, and phosphorus, the nitrogen indeed in considerable proportion (about 15-19 per cent). THERE TAKES PLACE ACCORDINGLY WITHIN PLANTS A NEW FORMATION OF ALBUMINOUS SUBSTANCES. There are certain indications that this formation is, in part, accomplished within the green cells of the leaves, but it must also be carried on in tissues devoid of chlorophyll.

As little is known concerning the process of the synthesis of the albuminous substances of plants as concerning the formation of the carbohydrates from the carbonic acid and water. It has generally been supposed that they are formed from the carbohydrates and mineral substances already mentioned, since these are known to be transported to the region where the formation of protoplasm occurs, and are there consumed. The carbohydrates utilised in this process seem to be principally GLUCOSE (both grape-sugar, dextrose, $C_6H_{12}O_6 + H_2O$, and fruit-sugar, lævulose, $C_6H_{12}O_6$) and MALTOSE ($C_{12}H_{22}O_{11} \times H_2O$) together with benzole derivatives; whatever may be the form of the original carbohydrate, whether starch, inulin, cane-sugar, reserve-cellulose, or glycogen, glucose or maltose is always first formed from it.

The mineral nitrates, sulphates, and phosphates take part in the process, chiefly in the form of potassium and magnesium salts. Nitrogen and sulphur are liberated from the nitrates and sulphates, with decomposition of the acid radicals; while of the phosphates, the acid group is utilised in the formation of nuclein. Iron, which is an essential for all plants whether or not they contain chlorophyll, appears to enter into the composition of the nuclein. According to recent experiments calcium salts appear to play a more immediate part in the proteid synthesis than was formerly supposed to be the case. Their importance, for most plants, is due to their functioning as a medium for conveying the mineral acids, and for neutralising or precipitating oxalic acid ($C_2H_2O_4$). The oxalate of potassium, which is first formed from the potassium nitrate, reacts with the calcium salts present, with the formation of calcium oxalate, which is only slightly soluble, and crystallises out as it accumulates. Wherever the formation of albumen or nuclein takes place, oxalic acid is formed, the calcium salts of which may usually be found in adjacent cells, in the form of aggregates of crystals, raphides, or crystal sand.

On account of their occurrence and behaviour in plants, the amides and hexa-carbon bases are regarded as preliminary stages in the formation of albuminous substances. Among the amides ASPARAGIN, $C_2H_3(NH_2)(CONH_2)(COOH)$, is noteworthy on account of its wide distribution. It is present in abundance in Gramineae and Leguminosae (one litre of sap from Bean seedlings contains about 12-15 grammes). In the Cruciferae and Cucurbitaceae it is replaced by glutamin, while in the Coniferae a hexa-carbon base (arginin, $C_6H_{14}N_4O_2$) appears to play the same role. Any real knowledge of the mode of origin and transformation into more complicated albuminous compounds of these and similar nitrogenous substances (*e.g.* betain, leucin, tyrosin, and allantoin) is at present wanting.

The colloidal nature of many albuminous substances, which hinders their osmotic diffusion, is of importance since it facilitates their recognition by appropriate reactions and their localisation in the protoplasm (42).

Transfer of the Products of Assimilation

When colloidal proteid substances are to be conveyed through the tissues, as, for example, from seeds rich in proteids into the seedlings, they are first by a hydrolytic process decomposed into soluble substances. According to SCHULZE (43), albumoses and peptone are first formed, and these are then broken up into amides and hexa-carbon bases, and sometimes even into compounds of ammonia. They are in this diffusible form transferred to places where, in combination with carbohydrates and mineral acids, they are used anew along with carbohydrates and salts in the formation of albumen.

In addition to the transfer of nitrogenous constructive material through the parenchymatous tissues, the LONG-DISTANCE TRANSPORT OF THE READY-FORMED ALBUMINOUS SUBSTANCES seems to take place through the open sieve-tubes of the bast. It appears to be in the sieve-tubes, which contain, during life, albuminous substances, starch grains, drops of oil and leptomin, that the conduction of organic substances is effected from the leaves. The increased thickening of the cortical layers observed just above wounds made by ringing trees, is due to the interruption and detention of a flow of nourishing sap through the phloem towards the roots.

The transfer of the carbohydrates through unbroken cell walls to the various points of consumption can only be accomplished when they are in solution. In case they are not already dissolved in the cell sap, they must first be converted into soluble substances capable of osmosis. This is of the highest importance for the transfer and utilisation of starch and reserve cellulose (hemicellulose). The former is converted by the influence of DIASTASE into glucose or maltose.

Diastase belongs to those peculiarly acting substances termed FERMENTS or ENZYMES, which possess the remarkable power of decomposing or transforming certain organic compounds without themselves becoming changed or consumed in the process. By virtue of this property they are enabled to transform unlimited quantities of certain substances if the resulting product is continuously removed. According to their most important physiological properties, diastatic, peptonising or proteolytic, and inverting enzymes are recognised, which act on starch, albuminous substances, and sugars respectively. These groups do not, however, exhaust the various ways in which these substances, which play such an important part in the chemical changes taking place in the organism, act. Thus there are trypsin-like ferments which dissolve albumen in an alkaline medium, ferments which dissolve membranes of cellulose, wood, or chitin, those that decompose glucosides and oils, and others that convert urea into ammonium carbonate (ureases). These and other enzymes have been found in plants, and there is no doubt that such bodies play a part in many imperfectly understood processes, especially in Fungi. A point which the enzymes named above have in common is their hydrolytic mode of action. They introduce the elements of water into the substance acted on, starch ($C_6H_{10}O_5$), for example, being converted into soluble glucose ($C_6H_{12}O_6$).

BUCHNER discovered that the expressed sap of the yeast-plant, even after being filtered, is able to transform grape-sugar into alcohol and carbonic acid. He ascribed this property to a special enzyme termed ZYMASE (alcoholase). The name of OXYDASES is given to certain substances which are regarded as acting by introducing oxygen.

Enzymes are for the most part colloidal albuminous substances which are formed from the protoplasm, and exhibit a so-called catalytic mode of action. They are easily rendered inactive by poisons or by too high a temperature. Inorganic substances (catalysators such as finely divided iridium or platinum) exhibit a similar catalytic action to enzymes; the power the latter possess of exciting fermentation is thus not due to any special vital property. They can act when removed from the organism, and may be precipitated from solution and again dissolved without loss of power. Besides ferments which hasten chemical reactions, others which arrest the reaction are known (paralysators), others oppose and inhibit the action of catalytic ferments (anti-ferments) ([44]).

Other substances similar to diastase, and also capable of transforming starch into dextrin, maltose or glucose, are widely distributed throughout the vegetable kingdom, and are classed together as diastatic ferments. They are especially abundant in starchy germinating seeds, as well as in tubers and bulbs, in leaves and young shoots. They have also been found, strange to say, in organs where there was no starch for them to act upon. The diastatic transformation and dissolution of the starch is accomplished in a peculiar manner. The starch grain is not dissolved as a homogeneous crystal, uniformly from the surface inwards, but becomes corroded by narrow canals, until it is finally completely disorganised, and falls into small pieces (Fig. 201).

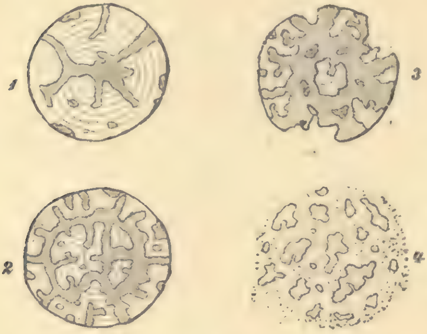


Fig. 201.—Different stages of corrosion shown by the starch grains of germinating Barley.

The complete transformation of the starch formed in the chlorophyll corpuscles during the day, takes place, as a rule, at night; for in the daytime the action of the diastatic ferment is counterbalanced by the formation of new starch. The glucose which is thus produced in the leaves passes out of the mesophyll cells into the elongated cells of the vascular bundle-sheaths and from them into the phloem. The glucose and maltose are transferred through the leaf-stalks into the stem. Thence they are conveyed to the young shoots and buds or carried down to the roots; in short, they are finally transported to places where they are required for the nutrition of the plant. The glucose and maltose often become converted into other carbohydrates, particularly into starch, during their passage from one organ to another. Starch thus formed from other carbohydrates, and not directly by assimilation, is often referred to as TRANSITORY STARCH, and is usually distinguishable by the smaller size of the grains.

For the purpose not of transport but of protection against cold starch is sometimes transformed into sugar (sweetening of potatoes) or oil (in the cortex and sometimes the wood of trees) (45).

The Storage of Reserve Material

All the products of assimilation are not at once consumed. In spite of this, however, assimilation is continued, and the surplus products beyond the requirements of immediate consumption are removed from the place of formation and accumulated as RESERVE MATERIAL for future use. In our herbs, bushes, and trees, as the yearly growth and consequent consumption cease towards the end of each vegetative period, and as the assimilating organs have by that time attained their greatest expansion and efficiency, the surplus of reserve material is greatest at the close of the season, and is stored in special RESERVOIRS OF RESERVE MATERIAL. The growth of the shoots and leaves of the next season and similarly the growth of seedling plants is dependent on such reserve materials. Reserve materials will accordingly be found stored in different forms in the cells of the embryo, or in the surrounding tissues of the seed, in underground rhizomes, tubers, bulbs, and roots, or in the cortical layers, the medullary rays, the wood parenchyma (especially the thin-walled fibres), and the medulla of persistent stems. Conveyed to these depositories of reserve material, the glucose and maltose are again converted into other carbohydrates, usually starch. In other cases the reserve carbohydrates take the form of cane-sugar (the sugar-beet contains 5-8 per cent, and selected varieties 18 per cent, and in some cases even 21 and 26 per cent), inulin (Compositae, Campanulaceae) or reserve cellulose (*e.g.* vegetable ivory in the fruit of *Phytelephas*). Still more remarkable is the transformation of carbohydrates into fats and oils, occurring in the ripe and ripening seeds of many plants, in fruits (Olive, oil-palm), and also in strictly vegetative tissues. In winter the starch in the wood of many trees also becomes converted into oil, but in the succeeding spring it is again changed to starch. It is finally, at the opening of the buds, converted into glucose or maltose, and conveyed by the transpiration current to the young shoots. Other receptacles of reserve material contain scarcely any carbohydrate, but on the other hand there is much more albuminous matter in the form of thick protoplasm, aleurone grains, protein crystals, and fats (seeds of *Ricinus*). That in germination similar tissues with protoplasm, nucleus, cell walls, etc., are formed from these different materials, seems to indicate that all these constructive materials are of almost equal value to the plants. This is due to the fact that plants can apparently without difficulty transform the carbohydrates, fats, or albuminous substances one into the other, a result not yet accomplished by chemical processes.

Other Products of Metabolism

The chemical activity of the vegetable cell is by no means exhausted in the production of the substances mentioned : the increasing number of chemical compounds found to be derived from the first product of assimilation is a matter of continual surprise. Of most of them neither the manner of their formation nor their full importance in metabolism is understood. The conditions are not even fully known which are necessary for the formation and functional activity of the ORGANIC ACIDS (malic, tartaric, citric, etc.) which may in part be considered as products of imperfect respiration while they are produced by some Fungi to acidify the medium in which they live and render it less favourable for competing organisms. The same holds for the equally widely-spread tannins. The function of the GLUCOSIDES is also imperfectly understood. These are compounds of sugars with a number of different substances. They are soluble in water, and by the action of ferments or dilute acids are broken up into glucose and other derivative products. It is conceivable that the formation of glucosides (and tannins) serves to locally fix substances which otherwise would readily diosmose. It might even be suggested that the polysaccharides, starch and cellulose, might be regarded as glucosides of the sugars themselves. In the Amygdalaceae (Bitter Almonds, Plum seeds) AMYGDALIN is found which on fermentation yields hydrocyanic acid in addition to benzaldehyde. The Lima or Java beans (*Phaseolus lunatus*), which of late years have been used for feeding cattle, also liberate from a glucoside hydrocyanic acid. In the wild form this may be in such quantity (0·16 per cent) that fatal poisoning has resulted. From a similar cause *Sorghum*, *Glyceria*, and *Lotus* may be more or less poisonous. Glucosides appear in the Solanaceae as the poisonous SOLANIN, in the Cruciferae (mustard seeds) as MYRONIC ACID, in the bark of the Horse-chestnut as extremely fluorescent ÆSCULIN, in species of *Digitalis* as the poisonous DIGITALIN, and in the cortex of Willows as SALICIN. Certain plants (*Indigofera*, *Polygonum tinctorium*) contain INDICAN, the glucoside of indoxyl ; the latter substance is converted by oxidation into indigo. Woad (*Isatis tinctoria*) contains, on the other hand, the related glucoside ISATIN (46). CONIFERIN, which is present in the cambial sap of the Conifers, has recently acquired an economic value, as from it VANILLIN, the aromatic principle of vanilla, may be artificially produced. In this process the coniferin is decomposed, through the action of a ferment or acid, into glucose and coniferyl-alcohol, by the oxidation of which its aldehyde, vanillin, is formed.

It is as yet unknown what part in the metabolic processes of plants is performed by the BITTER PRINCIPLES, such as the LUPULIN of Hops, ALOIN of Aloes, ABSYNTHIN of Wormwood. There is the same uncertainty with regard to the functions of the ALKALOIDS. Since most alkaloids, STRYCHNINE, BRUCINE, VERATRINE, CONIINE, MUSCARINE, ATROPINE, QUININE, MORPHINE, CODEINE, ACONITINE, COLCHICINE, NICOTINE, PILOCARPINE, COCAINE, together with CAFFEINE (theine) and THEOBROMINE which are closely related to uric acid, and many others are violent poisons, their vegetable bases and repugnant bitter principles furnish a certain protection to plants against destructive animals. This, however, does not preclude the possibility that they may at the same time have an important physiological significance. Thus, according to TREUB, hydrocyanic acid plays the same part in the formation and transport of proteids in *Pangium edule* as the amides do in other plants. It must, however, be noted that alkaloids are also poisonous to the protoplasm of the plant (47).

The COLOURING MATTERS AND ETHEREAL OILS, although in actual weight present only in small quantities, make themselves particularly noticeable to the senses of sight and smell. They probably represent only bye- and end-products of metabolism ; and, with the exception of chlorophyll, take no further part in the vital processes of plants, except in so far as they are beneficial to the general well-being by enticing (*e.g.* flowers, fruits) or repelling (*e.g.* by warning colours) animals. Their œcological significance is accordingly much better known than their physiological function. Just as the ethereal oils are frequently found in special excretory receptacles, the resins, gum-resins, and gum-mucilages, which are also excretion products, are usually deposited in canals or glandular cavities, and are often mixed with ethereal oils. Whether their formation in the particular instances is necessary for the carrying out of the normal processes of metabolism is altogether uncertain. They are, at any rate, useful to plants when wounded, serving as a protection against evaporation and the attacks of parasites. On a square centimetre of the surface of the splint-wood of the Pine, sixty to seventy resin canals open, and the wood contains, according to MAYR, 22 kilos. of resin in every cubic metre.

The significance of the so-called india-rubber (CAOUTCHOUC) and GUTTA-PERCHA in the latex in the economy of the plant is still less known. In addition to these substances, there also occur in latex, resins, ethereal oils, alkaloids (in opium), leptomin, starch grains, and other carbohydrates, oil-drops, and albuminous substances. The presence of these substances valuable as constructive material, and occasionally also of active enzymes (peptonising ferments are found in the milky juice of *Ficus Carica* and *Carica Papaya*), in the latex, gave rise to the suggestion that the latex cells and tubes function in the transport of the nutrient matter. Our present knowledge of these often caustic and poisonous saps is limited to their external utility in the economy of plant life. By their obnoxious properties they defend plants from the attacks of enemies. Also, in the event of plants being wounded, the latex is pressed out either by the surrounding turgescent tissue or by the tension of the elastic walls of its own cells, and forms, as it quickly coagulates in the air, an efficient covering for the wound. In other plants, especially in trees, wound-gum serves the same purpose. (Pp. 134, 151.)

Special Processes of Nutrition

Parasites, Saprophytes, Symbionts, and Insectivorous Plants.—The acquisition of organic nutritive substances through the activity of assimilating green cells is the most frequent, and is consequently considered the normal method of plant nutrition. Other modes of nutrition are only possible at the cost of organic substances already produced by the assimilatory activity of green plants. Some plants forego all attempts to develop an adequate chlorophyll apparatus, and by so doing become unable to provide themselves with nourishment from the inorganic matter about them.

Great numbers of such colourless plants derive their nourishment from the bodies of dead animals and plants. All organic matter at one time or another falls into the power of such plants as are devoid of chlorophyll; it is chiefly due to their decomposing activity in the performance of their nutritive processes that the whole surface of the earth is not covered with a thick deposit of the animal and plant remains of the past thousands of years. These peculiar plants are not satisfied with the possession of the lifeless matter alone; they even seize upon living organisms, both animal and vegetable, in their search for food.

It is chiefly the vast number of Bacteria and Fungi which nourish themselves in this way as PARASITES (upon living organisms) or as SAPROPHYTES (upon decaying remains of animals and plants and other organic substances). But even some species of the most widely separated families of the higher phanerogamic plants have also adopted this method of obtaining food.

As a result of this modification of their manner of life, the organisation and functions of these higher plants have undergone the most remarkable transformation. From the corresponding changes in their external appearance, it is evident how far-reaching is the influence exercised by the chlorophyll. With the diminution or complete disappearance of the chlorophyll, and consequent adoption of a dependent mode of life, the development of large leaf surfaces, so especially fitted for the work of assimilation, is discontinued. The leaves shrink to insignificant scales, for with the loss of their assimilatory activity the exposure of large surfaces to the light is no longer essential for nutrition. For the same reason active transpiration becomes unnecessary; the xylem portion of the vascular bundle remains weak, and secondary wood is feebly developed. In contrast to these processes of reduction resulting from a cessation of assimilation, there is the newly developed power in the case of parasites to penetrate other living organisms and to deprive them of their assimilated products. In saprophytic plants, however, where the question is merely one of absorbing nourishment from organic remains, the external adaptations for taking up nourishment continue more like those for absorbing the mineral salts from the soil, for it then depends only upon an intimate contact with the decaying substances.

Cuscuta europaea (Fig. 202), a plant belonging to the family of the Convolvulaceae, may be cited as an example of a parasitic Phanerogam. Although, through the possession of chlorophyll, it seems to some extent to resemble normally assimilating plants, in reality the amount of chlorophyll present is so small that it is evident that *Cuscuta* (Dodder) affords an example of a well-equipped parasite.

The embryonic *Cuscuta* plantlet, coiled up in the seeds, pushes up from the ground in the spring, but even then it makes no use of its cotyledons as a source of nourishment; they always remain in an undeveloped condition (Fig. 202 at the right). Nor does any underground root system develop from the young rootlet, which soon dies off. The seedling becomes at once drawn out into a long thin filament, the free end of which moves in wide circles, and so inevitably discovers any plant, available as a host, that may be growing within its reach. In case its search for a host plant is unsuccessful, the seedling is still able to creep a short distance farther at the expense of the nourishing matter drawn from the other extremity of the filament, which then dies off (*t*) as the growing extremity lengthens. If the free end, in the course of its circular movements, comes ultimately into contact with a suitable host plant, such as, for example, the stem of a Nettle or a young Willow shoot (Fig. 202 in the centre), it twines closely about it like a climbing plant. Papillose protuberances of the epidermis are developed on that side of the parasitic stem in contact with the host plant, and pierce the tissue of the host. If the conditions are favourable, these PRE-HAUSTORIA are soon followed by special organs of absorption, the HAUSTORIA (*H*). These arise from the internal tissues of the parasite, and possess, in a marked degree, the capability of penetrating to a considerable depth into the body of the host plant by means of solvent ferments and the pressure resulting from their own growth. They invade the tissues of the host, apparently without difficulty, and fasten themselves closely upon its vascular bundles, while single hypha-like filaments produced from the main part of the haustoria penetrate the soft parenchyma and absorb nourishment from the cells. A direct connection is formed between the xylem and phloem portions of the bundles of the host plant and the conducting system of the parasite, for in the thin-walled tissue of the haustoria there now develop both wood and sieve-tube elements, which connect the corresponding elements of the host with those of the parasitic stem (Fig. 202 at the left). Like an actual lateral organ of the host plant, the parasite draws its transpiration water from the xylem, and its plastic nutrient matter from the phloem of its host.

The seeds of *Orobanche* (Broom rape), another parasite, only germinate when in contact with the roots of the host plant; its haustoria only penetrate the roots, and only its light yellow, reddish-brown or amethyst-coloured flower-shoot appears above the surface of the ground. *Orobanche*, like *Cuscuta*, contains a small amount of chlorophyll. Both are dreaded pests; they inflict serious damage upon cultivated plants, and are difficult to exterminate.

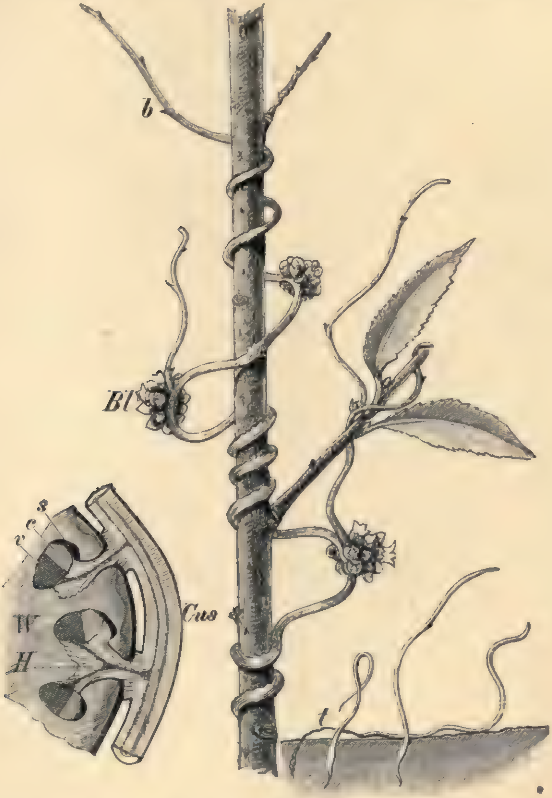


FIG. 202.—*Cuscuta europaea.* On the right, germinating seedlings. In the middle, a plant of *Cuscuta* parasitic on a Willow twig; *b*, reduced leaves; *Bl*, flower-clusters. On the left, cross-section of the host-plant *W*, showing haustoria *H* of the parasite *Cus*, penetrating the cortical parenchyma and in intimate contact with the xylem *v* and the phloem *c* of the vascular bundles; *s*, displaced cap of sheathing sclerenchyma.

Many exotic parasitic plants, especially the Rafflesiaceae, have become so completely transformed by their parasitic mode of life that they develop no apparent vegetative body at all; but grow altogether within their host plant, whence they send out at intervals their extraordinary flowers. In the case of *Pilostyles*, a parasite which lives on some shrubby Leguminosae, the whole vegetative body is broken up into filaments of cells which penetrate the host plant like the mycelium of a fungus. The flowers alone become visible and protrude from the stems and leaf-stalks of the host plant (Fig. 203) (48).

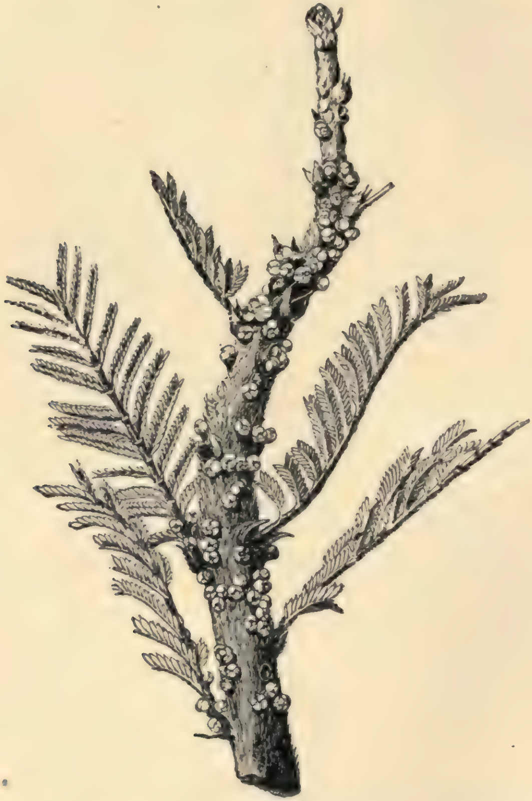


FIG. 203.—Branch of a leguminous plant from the surface of which the flowers of a parasitic plant (*Pilostyles Ulei*, Solms) are protruding. (From GOEBEL's *Organography*.)

In contrast to these parasites, which have come to be absolutely dependent upon other plants for their nourishment, there are certain parasites which, to judge by external appearances, seem to be quite independent, for they possess large green leaves with which they are able to assimilate vigorously. In spite of this, however, the plants only develop normally, when their root system is in connection with the roots of other plants by means of disc-shaped haustoria. They may even (as is also the case with *Cuscuta*) enter into this relation with other individuals of the same species. *Thesium*, belonging to the Santalaceae, and the following genera of the Rhinanthaceae, *Rhinanthus*, *Euphrasia*, *Pedicularis*, *Bartsia*, and *Tozzia* may be mentioned as examples of plants showing these peculiar conditions. In *Tozzia* the parasitism is well marked in the earliest developmental stages. The Mistletoe (*Viscum album*), although strictly parasitic, possesses, nevertheless, like many of the allied foreign genera of the Loranthaceae, fairly large leaves well supplied with chlorophyll, and fully able to provide all the carbohydrates required. It obtains, however, from the host plant (as HEINRICHER has also shown to be probable in the case of the Rhinanthaceae) its supply of water and dissolved salts. Another member of the Rhinanthaceae, *Melampyrum*, though primarily a root parasite, has, on the other hand, adopted a saprophytic mode of life (⁴⁹).

Humus plants, like some of the Orchidaceae (*Neottia*, *Coralliorrhiza*, etc.), and the Monotropeae, are restricted to a purely saprophytic mode of nutrition, and to that end utilise the leaf-mould accumulated under trees.

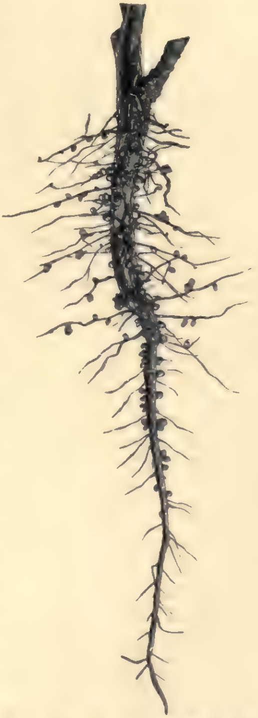


FIG. 204.—A root of *Vicia Faba*, with numerous root-tubercles. (Reduced.)

The roots and rhizomes of these saprophytes stand in most intimate relation with fungal hyphæ. The same indeed holds for the majority of green plants which grow in woods and heaths, where the soil is rich in humus. The fungal hyphæ are sometimes present in coiled masses within the cells of a definite zone of the cortex, only occasional filaments passing outwards to the soil. In other cases the fungus surrounds the young roots with a dense investment of interwoven hyphæ. The former arrangement is spoken of as ENDOTROPHIC, the latter as EXOTROPHIC MYCORHIZA; the two types are, however, connected by intermediate forms. A direct exchange of substance between the soil and the root would appear impossible in the case of the exotrophic mycorhiza. On this ground, and because, despite the reduced surface exposed to the humus-containing soil by the roots or rhizomes of total saprophytes, these obtain sufficient nutriment, a co-operation of the fungus in the nutrition of such plants has been assumed. The results of culture experiments lend further support to this view. Little is known, however, as to the nature of the relation between the fungus and the saprophyte. The view of PERCY GROOM and JANSE that in the case of endotrophic mycorhizas the fungus supplies combined nitrogen, *i.e.* is ultimately digested by the root, is supported by the work of W. MAGNUS, SHIBATA, and HILTNER. STAHL on the other hand sees its use in a better supply of salts from the soil. The latter view, however, could only be a sufficient explanation in the case of green plants (⁵⁰).

The relation between roots and certain Bacteria in the case of the Leguminosae is better understood. It has long been known that peculiar outgrowths, the so-called ROOT-TUBERCLES, are found on the roots of many Leguminosae (Bean, Pea, Lupine, Clover, etc.) (Fig. 204). These tubercles, of which a single bean plant may bear 4000, are caused by certain Bacteria (*Bacillus radicicola*, the two forms of which are distinguished by HILTNER as *Rhizobium radicicola* and *R. Beyerincki*). These Bacteria penetrate through the root-hairs into the cortex of the roots, and there give rise to the tubercular growths. These tubercles become filled with a bacterial mass, consisting principally of swollen and abnormally developed (hypertrophied) BACTERIOIDS, but in part also of Bacteria, which have remained in their normal condition. The former seem to be eventually consumed by the host plant, while the latter remain with the dead roots in the soil, to provide for future reproduction. As the experiments of HELLRIEGEL and the investigations of NOBBE, BEYERINCK, HILTNER, and others prove, we have here a case of mutual parasitism like those termed symbiosis by DE BARY. While the Bacterium lives on carbohydrates and at first also on albuminous substances supplied by the host plant, the latter profits by the power of fixing free nitrogen possessed by the Bacteria. This is effected by means of an enzyme demonstrated by HILTNER. While the Bacteria remain alive they furnish a steady supply of nitrogenous substance to the leguminous plant, and ultimately the remaining substance of the degenerated Bacterioids is absorbed. When the large amount expended on nitrogenous manures (Chili-saltpetre and ammonium sulphate) is borne in mind the agricultural importance of this natural fixation of nitrogen will be evident. It has been attempted to further it by infecting fields with soil rich in the bacteria or with pure cultures of specially active forms ("nitragin"). The fact that the tubercle-forming Leguminosae, unlike most plants, could flourish on ground poor in nitrogen, and could accumulate stores of reserve proteids was known in the time of Pliny, and these plants have long been known to form crops which enrich the soil by this accumulation of nitrogen ([51]).

If the soil in which such a leguminous plant grows contains a sufficiency of nitrates, few tubercles are formed on the roots. A similar immunity against infection is obtained by plants which bear a number of actively functional tubercles. In addition to the Leguminosae (in which order only *Gleditschia triacanthos* has as yet been found free from tubercles) tubercle formation due to a symbiosis with a lower organism is known in *Elaeagnus* and *Alnus*. According to NOBBE and HILTNER, these plants can also utilise free nitrogen. These authors have also shown experimentally that the same holds for *Podocarpus*, which possesses mycorhiza. Nitrogen-fixing Bacteria such as *Azotobacter chroococcum* are also found according to BENECKE and KEUTNER in the sea; according to REINKE they lodge in numbers in the mucilaginous coatings of Sea-weeds.

While among the higher plants only isolated forms have become total parasites or saprophytes, while in others the parasitism or saprophytism is occasional or partial, among the lower plants large families with numerous genera and species are found completely devoid of chlorophyll (Fungi and Bacteria), and wholly parasitic or saprophytic in their mode of life. Of the Fungi and Bacteria some are true parasites, and are often restricted to certain special plants or animals, or even to distinct organs; others, again, are strictly saprophytic in their habit, while others may be either parasitic or saprophytic, according to circumstances. What renders the conduct of these lower organisms particularly striking is the peculiarity possessed by many of them of not fully utilising all of the organic matter at their disposal; but, on the contrary, so decomposing and disorganising the greater part of it by their fermentative activity that, while at first competitors are inhibited, later their own development soon becomes restricted. When a mould attacks an apple, it not only takes the small amount of organic matter necessary for its sustenance, but at the same time converts the whole apple into a soft decaying mass upon which the fungus itself cannot exist. A considerable degree of heat is also evolved in the course of these processes. The utilisation of the heat produced in decomposing manure in making hot-beds is a familiar practice. The heat produced by damp fermenting hay or raw cotton may often become so great that in presence of inflammable gases spontaneous combustion ensues. In germinating Barley an increase in temperature of from 40 to 70 or more degrees has been observed. The development of so much heat in this case is not due solely to the respiration of the barley seeds, but according to COHN, to the decomposing activity of a fungus (*Aspergillus fumigatus*). The spontaneous combustion of raw cotton is, on the other hand, caused by a *Micrococcus*. Coagulated albumen and thick gelatine are rendered fluid by many Fungi and Bacteria, while the escaping gases (carbonic acid, sulphuretted hydrogen, ammonium sulphide, ammonia, etc.) show how far-reaching the decomposition is. In the same way *Penicillium brevicaule* and other Fungi can liberate poisonous arsenical gases when living on a substratum containing arsenic such as the green pigments of wall-papers. In this way by GOSIO'S method minute quantities of arsenic can be detected ([52]). It is by similar processes of decomposition that dead organic matter becomes thoroughly disorganised and rendered harmless. To the poisonous bye-products formed by Fungi and Bacteria is due the severity of many diseases which they produce in living organisms (potato disease, wheat smut, cholera, typhus, diphtheria, anthrax, etc.). By the possession or formation of substances, which react as specific poisons upon the infecting Bacteria, plants, and particularly animals, in turn protect themselves against the attacks of such micro-organisms. It is due to a knowledge of this fact that the science of Therapeutics has been enabled to cope more and more successfully with infectious diseases.

Fungi and Bacteria, in addition to the power, dangerous to themselves, of disorganising their own nutrient substratum by fermentation and putrefaction, also possess the capability of making an unsuitable substratum suitable for their sustenance. By means of inverting ferments they can convert an unsuitable cane-sugar into an available grape-sugar, and by their diastatic ferments they are able to form glucose and maltose from starch, and even from cellulose.

Many Fungi and Bacteria are practically omnivorous, while others are extremely exclusive in their selection of a substratum. Thus from ordinary tartaric acid *Penicillium* only utilises the dextro-rotatory form, and *Bacillus subtilis* only the lævo-rotatory form. *Aspergillus* growing in a mixture of glucose and glycerine utilises the former first ("election" of nutritive materials). If the glycerine alone is given it is completely utilised.

As is evident from their thriving upon such various substrata, Fungi have the power of producing from the different carbon compounds (and also from nitrogenous mineral compounds, such as ammonium tartrate, or even ammonium carbonate) protoplasm, cell wall, nuclein, fat, glycogen, etc.

While many Fungi inflict far greater injury upon their host plants by the decomposition they induce than by the withdrawal of the nutritive substances, others produce a different effect. The Rust-fungi, and the Agaricinae which attack trees, for instance, do comparatively little injury to their host; while the relation between host and fungus in the case of the Lichens has been shown to be absolutely beneficial. The Lichens were formerly considered to be a third group of the lower Cryptogams and of equal value with the Algae and Fungi. It is only comparatively recently that the discovery was made by DE BARY and verified by the investigations particularly of SCHWENDENER and STAHL, that the body of the Lichens is not a single organism, but in reality consists of Algae (*e.g.* Cyanophyceae), which also exist in a free state, and of Fungi, which for the most part belong to the Ascomycetes; these Fungi only exceptionally exist apart from the Lichen. The fungal hyphæ within the Lichen weave themselves around the Algae; and while the latter occupy the upper or outer side of the leaf-like or cylindrical thallus as the more favourable position for assimilation, the hyphæ come into the closest contact with them and absorb from them part of their assimilated products. The fungi in return provide the Algae with water, which, owing to the acids excreted, is often rich in nutrient salts, and enable them to live in situations in which they could not otherwise exist. The researches of ARTARIS make it probable that peptone is also provided by the fungus. As a result of this close union with the fungi, the Algae are in no way exhausted, but become more vigorous than in their free condition, and reproduce themselves by cell division. As both symbionts, the Algae as well as the Fungi, thus derive mutual advantage from their consortism, Lichens form one of the most typical examples of vegetable symbiosis ([53]).

The significance of the Cyanophyceae *Nostoc* and *Anabaena* in the roots of the Cycadaceae and in the leaves of *Azolla* and other water plants is still unknown ([54]).

In connection with these cases of symbiosis between plants, mention may here be made of the similar symbiotic relation existing between animals and plants. Like the Lichen-fungi, lower animals, according to BRANDT, profit by an association with unicellular Algae by appropriating their assimilated products without at the same time disturbing the performance of their functions. Freshwater Polyps (*Hydra*), Sponges (*Spongilla*), Ciliata (*Stentor*, *Paramecium*), also Heliozoa, Planaria, and *Amoebae* (*A. proteus*) are often characterised by a deep green colour, due to the numerous Algae which they harbour within their bodies, and from the products of whose assimilation they also derive nourishment. In the case of the Radiolarians, the so-called "yellow cells," which have been distinguished as yellow unicellular Seaweeds, function in the same way as the green Algae in the other instances. Another remarkable example of symbiosis in which the relationship is not one merely of simple nutrition, has been developed between certain plants and ants. The so-called ANT-PLANTS (Myrmecophytes) offer to certain small, extremely warlike ants a dwelling in convenient cavities of the stems (*Cecropia*), in branches (*Triplaris*) in hollow thorns (*Acacia spadicigera* and *sphaerocephala*, Fig. 205), in swollen and inflated internodes (*Humboldtia laurifolia*, Fig. 206), or in the labyrinthine passages of their large stem-tubers (*Myrmecodia*, Fig. 207). At the same time the ants are provided with food in the case of the Cecropias and Acacias in the form of albuminous fatty bodies ("food bodies," Fig. 205 *F*), and by the Acacias also with nectar (Fig. 205, *N*). The ants in exchange guard the plants most effectively against the inroads of animal foes as well as against other leaf-cutting species of ants, which, in the American tropics, kill trees by completely and rapidly divesting them of their entire foliage. These leaf-cutting ants, as was shown by BELT and MÖLLER, live in symbiosis with a Fungus (*Rozites gongylophora*). Upon the accumulated leaves ("Fungus-gardens"), the ants make pure cultures of a fungus mycelium, whose peculiar nutritive outgrowths serve them exclusively for nourishment. Termites have more recently been discovered to be Fungus cultivators (55). Other familiar examples of symbiosis are those existing between flowers and birds or insects. The flowers in these instances provide the nourishment, usually nectar or pollen, but sometimes also the ovules (Yucca-moth and the gall-wasp of the Fig), while the animals are instrumental in the pollination. Here also each symbiont is dependent upon the other. In the case of the unintentional dissemination of fruits and seeds by the agency of animals, the symbiotic relations are less close.

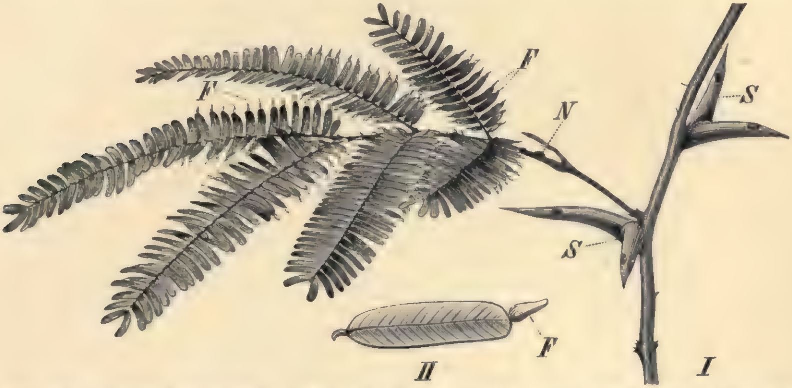


FIG. 205.—*Acacia sphaerocephala*. *I*, Leaf and part of stem ; *S*, hollow thorns in which the ants live ; *F*, food bodies at the apices of the lower pinnules ; *N*, nectary on the petiole. (Reduced.) *II*, Single pinnule with food-body, *F*. (Somewhat enlarged.)

Of all the different processes of supplementary nutrition employed by plants, those exhibited by Carnivorous or Insectivorous Plants in the capture and digestion of animals are unquestionably the most curious. Although they are green plants and able to manufacture carbohydrates for themselves they have, in addition, secured for themselves, by peculiar contrivances, an extraordinary source of nitrogenous organic matter, by means of which they are enabled to sustain a more vigorous growth and especially to produce more seeds than would otherwise be possible without animal nourishment.

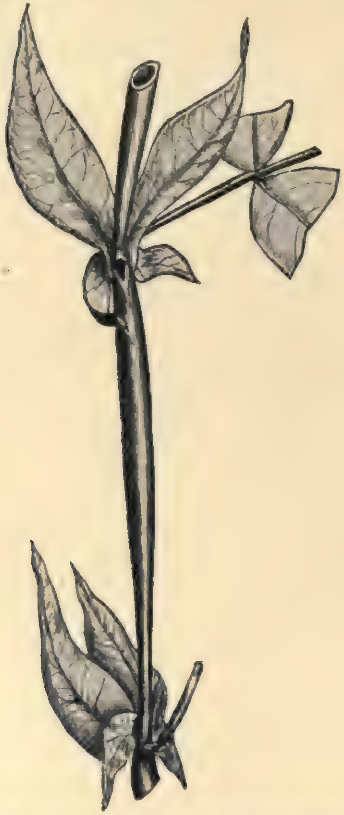


FIG. 206.—*Humboldtia laurifolia*, showing the entrance to the hollow internode. (From SCHIMPER'S *Plant-Geography.*)

It is not accidental that the plants which have become carnivorous are, for the most part, either inhabitants of damp places, of water or swamps, and moist tropical woods, or that they are epiphytes. The nitrogenous and phosphoric salts of the soil are not obtained by them in the same quantities as in the case of the more vigorously transpiring land plants. This is very evidently the case in the Sundew (*Drosera*), which is loosely attached by a few roots upon a thick spongy carpet of Bog-moss, and must find in the animal food a valuable addition to its nitrogenous nourishment.

A great variety of contrivances for the capture of insects are made use of by carnivorous plants. The leaves of *Drosera* are covered with stalk-like outgrowths ("tentacles"), the glandular extremities of which discharge a viscid acid secretion (Fig. 208). Any small insect, or even larger fly or moth, which comes in contact with any of the tentacles is caught in the sticky secretion, and in its ineffectual struggle to free itself it only comes in contact with other glands and is even more securely held. Excited by the contact stimulus, all the other tentacles curve over and close upon the captured insect, while the leaf-lamina itself becomes concave and surrounds the small prisoner more closely. The secretion is then discharged more abundantly, and contains, in addition to an increased quantity of acid, a peptonising ferment. The imprisoned insect, becoming thus completely covered with the secretion, perishes. It is then slowly digested, and, together with the secretion itself, is absorbed by the cells of the leaf.

In *Pinguicula* it is the leaf-margins which fold over any small insects that may be held by the minute epidermal glands. In species of *Utricularia* (Fig. 47), growing frequently in stagnant water, small green bladders (metamorphosed leaf-segments) are found on the dissected leaves. In each bladder there is a small opening closed by an elastic valve which only opens inwards. Small snails and crustaceans can readily pass through this opening, guided to it by special outgrowths; but their egress is prevented by the trap-like action of the valve, so that in one bladder as many as ten or twelve crustaceans will often be found imprisoned at the same time. The absorption of the disorganised animal remains seems to be performed by forked hairs which spring from the walls of the bladder.

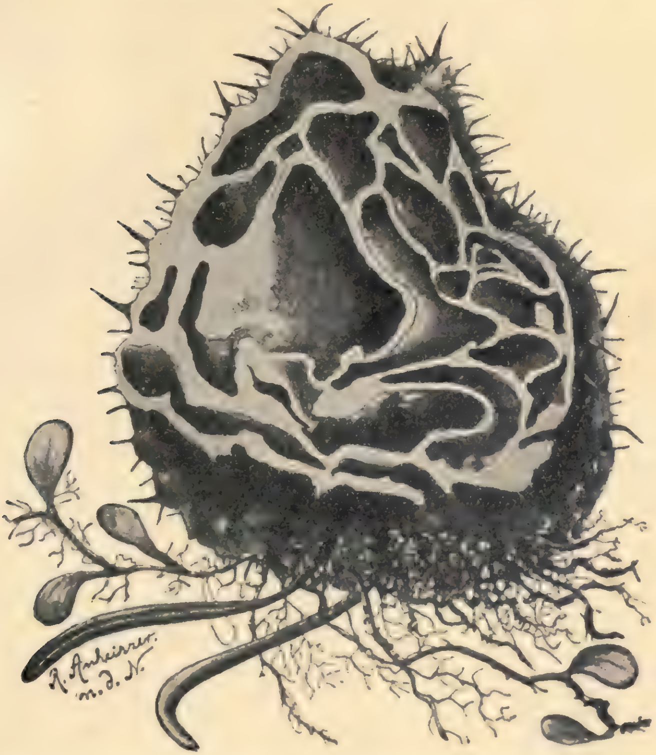


FIG. 207.—*Myrmecodia echinata*. Tuberous stem cut through longitudinally. Another epiphyte is seen below. (½ nat. size; from SCHIMPER's *Plant-Geography*.)

More remarkable still, and even better adapted for its purpose, is the mechanism exhibited by some exotic insectivorous plants. In the case of Venus' Fly-trap (*Dionaea*), growing in the peat-bogs of North Carolina, the capture of insects is effected by the sudden closing together of the two halves of the leaves (Fig. 209). This action is especially due to the irritability of three bristles on the upper side of each half-leaf (the leaf surfaces themselves are much less sensitive). Upon the death of the insect caught by the leaf, a copious excretion of digestive sap takes place from glandular hairs on the leaf surface, followed by the absorption of the products of the digestive solution. In the case of other well-known insectivorous plants (*Nepenthes*, *Cephalotus*, *Sarracenia*, *Darlingtonia*), the traps for the capture of animal food are formed by the leaves which grow in the shape of pitchers (Figs. 46, 210). These trap-like receptacles are partially filled with a watery fluid excreted from glands on their inner surfaces. Enticed by secretions of honey to the rim of the pitcher (in the case of *Nepenthes*), and then slipping on the extraordinarily smooth surface below

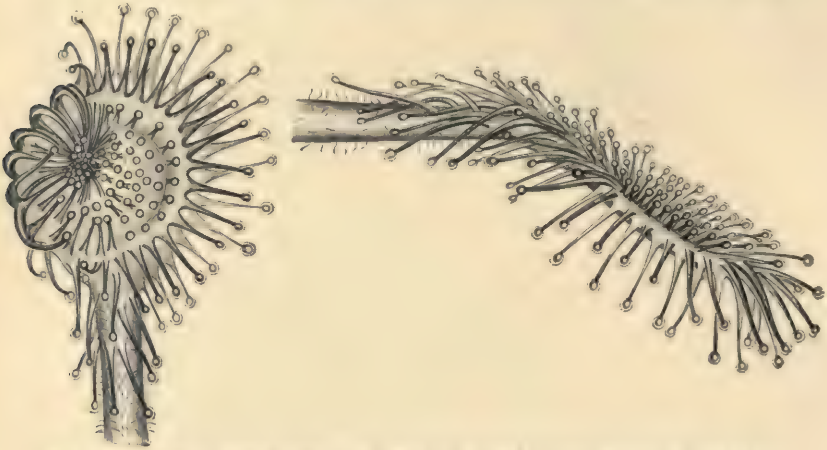


Fig. 208.—Leaves of *Drosera rotundifolia*. That on the left is viewed from above, that on the right from the side. (After Darwin enlarged.)

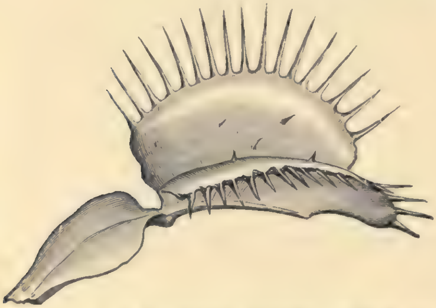


Fig. 209.—A leaf of *Dionaea muscipula*, showing the sensitive bristles on its upper surface, which, in the parts shaded, is also thickly beset with digestive glands. (After Darwin, enlarged.)

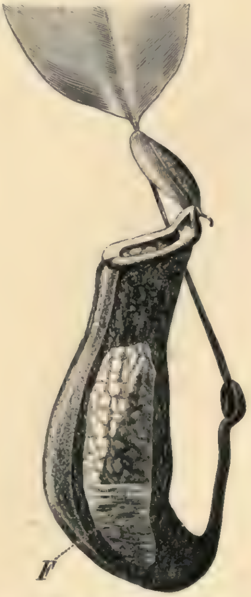


Fig. 210.—Pitchered leaf of a *Nepenthes*. A portion of the lateral wall of the pitcher has been removed in order to show the fluid (*F*), excreted by the leaf-glands. (Reduced.)

the margin, or guided by the downwardly-directed hairs, insects and other small animals finally fall into the fluid and are there digested by the action of ferments and acids. The larvæ which CLAUTRIAU found living in *Nepenthes* pitchers may, like intestinal parasites, be enabled to live under the conditions by secreting a protective anti-ferment. In *Sarracenia* and *Cephalotus*, GOEBEL was unable to discover any digestive ferments; but in *Cephalotus* it was possible to determine that the secretions have antiseptic properties. The lid-like appendage at the opening of the pitcher of *Nepenthes*, *Sarracenia*, and *Cephalotus* does not shut; its function seems to be merely to prevent foreign substances from falling into the pitcher, and particularly to keep out the rain. The entrance to the tubular leaves of *Darlingtonia* is under the helmet-like extremity, and therefore a lid is unnecessary (56).

III. Respiration

It is a matter of common knowledge that animals are unable to exist without breathing. In the higher animals the process of respiration is so evident as not easily to escape notice, but the fact that plants breathe is not at once so apparent. Just as the method of the nutrition of green plants was only discovered by experiment, so it also required carefully conducted experimental investigation to demonstrate that PLANTS ALSO MUST BREATHE IN ORDER TO LIVE; that, like animals, they take up oxygen and give off carbonic acid. Although the question had already been thoroughly investigated by SAUSSURE in 1822, and by DUTROCHET in 1837, and its essential features correctly interpreted, LIEBIG pronounced the belief in the respiration of plants to be opposed to all facts, on the ground that it was positively proved that plants on the contrary decomposed carbonic acid and gave off the oxygen. He asserted that it was an absurdity to suppose that both processes were carried on at the same time; and yet that is what occurs.

ASSIMILATION AND RESPIRATION ARE TWO DISTINCT VITAL PROCESSES CARRIED ON INDEPENDENTLY BY PLANTS. WHILE IN THE PROCESS OF ASSIMILATION **GREEN** PLANTS ALONE, AND ONLY IN THE LIGHT, DECOMPOSE CARBONIC ACID AND GIVE OFF OXYGEN, **ALL** PLANT ORGANS WITHOUT EXCEPTION BOTH BY DAY AND BY NIGHT TAKE UP OXYGEN AND GIVE OFF CARBONIC ACID. Organic substance, obtained by assimilation, is in turn lost by respiration. A seedling grown in the dark so that assimilation is impossible, loses by respiration a considerable part of its organic substance, and its dry weight is considerably diminished. It has been found that during the germination of a grain of Indian Corn, a full half of the organic reserve material is consumed in three weeks. That green plants growing in the light accumulate a considerable surplus of organic substance is due to the fact that the daily production of material by the assimilatory activity of the green portions is greater than the constant loss which is caused by the respiration of all the organs. Thus, according to BOUSSINGAULT'S estimates, in the course of one hour's assimilation a plant of Sweet Bay will produce material sufficient to cover thirty hours' respiration. Plants produce in twenty-four hours about five to ten times their own volume of carbonic acid. In shade-plants, according to GRIFFON, this is usually reduced to twice the plant's volume, while the commonly cultivated *Aspidistra* produces only one-half its own volume, and can therefore succeed even under conditions which are unfavourable to assimilation (57).

A means of judging of the importance of respiration is afforded by the behaviour of the plants themselves when deprived of oxygen. By placing them, for example, under a jar containing either pure nitrogen or hydrogen, or in one from which the air has been exhausted, it will be found that all vital activity soon comes to a standstill; plants, previously growing vigorously, cease their growth; the streaming motion of the protoplasm in the cells is suspended, as well as (with few exceptions, *e.g. Mimosa* and *Drosera*) all external movement of the organs. If oxygen be admitted, after not too long an interval, the interrupted performance of the vital functions is again renewed. A longer detention in an atmosphere devoid of oxygen will, however, irrevocably destroy all traces of vitality; as in every condition of rigor internal chemical changes take place which, by a prolonged exclusion of oxygen, lead to the destruction and disorganisation of the living substance. THE PRESENCE OF OXYGEN IS NECESSARY TO THE CHEMICAL PROCESSES TAKING PLACE WITHIN THE CELL, IN ORDER TO MAINTAIN THE LIVING SUBSTANCE IN A CONDITION OF NORMAL ACTIVITY.

The absorption of oxygen and the evolution of carbonic acid by living plants can be demonstrated both qualitatively and quantitatively by simple experiments. From what has already been said of the antagonistic nature of assimilation and respiration, it will be at once apparent that these experiments must be conducted either in the dark or on portions of plants devoid of chlorophyll. The more abundant the protoplasm and the more energetic its vital activity, so much the more vigorous is the respiration. The best results are obtained, therefore, from young portions of plants in an active state of growth. It should also be mentioned that in the following experiments only the carbonic acid and not the whole of the products of the respiratory activity are determined. From theoretical considerations, and also from exact chemical analysis, it has been definitely established that, IN ADDITION TO CARBONIC ACID, WATER IS FORMED FROM THE ORGANIC MATTER BY RESPIRATION.

The absorption of oxygen and the formation of carbonic acid may be clearly shown by the following experiment (Fig. 211). A flask (*B*) partly filled with young mushrooms or flower heads of a Composite is inverted with its mouth in an open vessel of mercury (*Q*), and a few centimetres of caustic potash solution (*K*) introduced within its neck. In the same degree as the carbonic acid produced by respiration is absorbed by the caustic potash, the volume of air in the flask will be reduced and the mercury will rise in the neck. After a time, the ascent of the mercury ceases and it remains stationary. If the quantity of air remaining in the flask be estimated, it will be found that it has lost a fifth of its original volume ; this means that the whole of the oxygen (which makes up one-fifth of the atmospheric air) has been absorbed. If caustic potash is not used in this experiment to absorb the exhaled carbonic acid, the mercury remains at its original level, or, in other words, the volume of air in the flask remains unchanged. From this experiment it is apparent that the volume of oxygen absorbed is equal to the volume of carbonic acid evolved, as expressed by the formula $\frac{CO_2}{O_2} = 1$. This equivalence of volume between the oxygen absorbed and the carbonic acid exhaled exists only in cases where the oxygen is used exclusively for complete respiration, and not where it is consumed in transforming the contents of the cells, as is observed in the germination of seeds rich in fat, and in the interchange of gases in the case of the succulents. In the germination of seeds rich in fat, the fat is converted into carbohydrates richer in oxygen. The oxygen consumed remains combined in the plant. On the other hand, in the case of the succulents the production of CO_2 falls with the formation of organic acids (malic acid in the case of the Cactaceae, oxalic acid in the Mesembryanthaceae) in the dark ; these acids are, however, again decomposed in the light and, according to AD. MAYER, starch is formed and oxygen set free. The respiratory co-efficient may further vary within certain limits according to the nutrition and conditions of cultivation of a plant.

The absorption of oxygen in the respiration of plants can also be shown by the fact that a flame, held in a receptacle in which plants have been kept for a time, is extinguished. If a lighted taper be thrust into a glass cylinder which has been partially filled with flowers or mushrooms and then tightly covered and allowed to remain for a day, it will be extinguished, as the oxygen of the air in the cylinder will all have been absorbed. The carbonic acid exhaled in respiration can be quantitatively determined from the increase in the weight of the caustic potash by which it has been absorbed, or by conducting the respired carbonic acid gas through baryta water and estimating the precipitate of barium carbonate.

Intramolecular Respiration (58).—In 1871 AD. MAYER showed that the yeast-plant could obtain the chemical energy necessary for its life from changes within its organic substance and without absorbing oxygen. In the middle of the 'seventies PFLÜGER made the discovery that frogs are not only able to live for some time in an atmosphere devoid of oxygen, but even continue to exhale carbonic acid. From similar investigations it was found that the higher plants also, when deprived of oxygen, do not die at once, but can prolong their life for a time and evolve carbonic acid. Under these circumstances it is apparent that both elements, the carbon as well as the oxygen, must be derived from the organic substance of the plants themselves : the oxygen can only be obtained through some unusual process of decomposition carried on within the plant. This form of respiration has consequently been described as intramolecular (anaerobic) respiration.

The amount of carbonic acid produced in a given time by intramolecular respiration is usually less ($\frac{1}{3}$-$\frac{2}{3}$) than that given off in the same time during normal respiration. There are plants, however (for instance, *Vicia Faba*), whose seedlings, in an atmosphere of pure hydrogen, will exhale for hours as much carbonic acid as in the ordinary air. During intramolecular respiration in aerobionts all growth ceases and abnormal processes of decomposition take place, whereby, as for instance in alcoholic fermentation, alcohol and other products are formed.

Intramolecular respiration commences as soon as the access of free oxygen to the protoplasm is prevented, and continues until the latter is killed by the accumulation of injurious products of decomposition. The sufficiently early readmittance of oxygen may, however, permit the cell to resume its normal condition by reestablishing ordinary respiration and removing the accumulated products of decomposition.

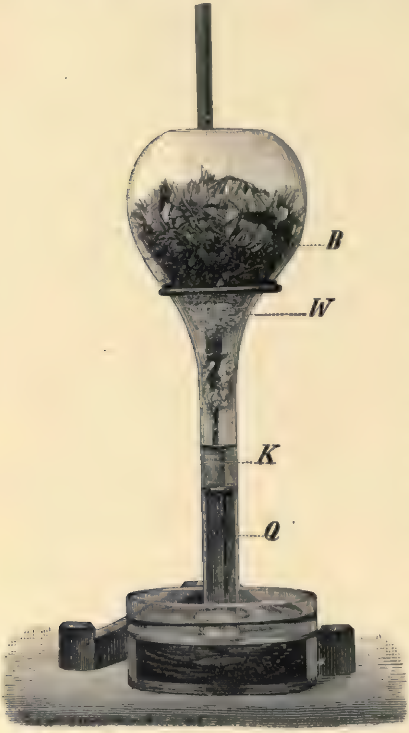


FIG. 211.—Experiment to demonstrate respiration. The inverted flask (*B*) is partially filled with flowers, which are held in place by the plug of cotton (*W*). Through the absorption of the carbonic acid exhaled in respiration, by the solution of caustic potash (*K*), the mercury (*Q*) rises in the neck of the flash.

Some plants endure the absence of free oxygen badly and only for a short time, others better and for a longer period. Certain of the lower plants (Bacteria, Fungi, Characeae) can exist for a considerable time without free oxygen, or are even able under favourable conditions to find in intramolecular respiration a complete substitute for the ordinary oxygen-respiration. This capability is so extreme in some Bacteria that no trace of free oxygen is necessary for their existence, while some cannot live in the presence of oxygen. To distinguish such specially adapted organisms from those which depend for their normal respiration on free oxygen (aerobionts or aerobes) they are termed anaerobionts or anaerobes. The grades of independence of free oxygen indicated above may be distinguished as temporary or facultative anaerobiosis and permanent or obligate anaerobiosis respectively. Plants which can store up substances rich in oxygen (*e.g.* certain pigments) and at the expense of these live for a time without an external supply of oxygen may be distinguished as pseudo-anaerobes.

Respiration as a Source of Energy.—That the metabolic change constituting respiration is a necessary concomitant of life may be inferred from the cessation of vital manifestations when respiration is interfered with, and the association of more active life with increased demands on the respiratory process.

In respiration chemical changes occur leading to the setting free of energy. It is hardly too much to say that it is the energy obtained by respiration which serves to carry on and maintain the vital manifestations. Thus a specific vital energy is obtained by means of respiration, which might be termed vital force were this term not used in another sense ; such a supply of energy is not provided by other sources of force in the plant (force of pressure in turgescence, vibrations of light and heat rays, etc.).

The majority of plants sacrifice in physiological combustion a portion of their organic substance (especially carbohydrates) in order to obtain this driving power. The combustion is as a rule so complete that CO_2 and H_2O are the resulting products ; this not only obtains the maximum of energy but obviates the accumulation of injurious products of respiration. In other cases, however, considerable amounts of organic acids are formed. This modification, which is found in succulents living under unfavourable conditions for gaseous exchange and consequently for assimilation, avoids the loss of carbon attendant on the liberation of CO_2 into the air. (Cf. p. 241).

The energy liberated by the respiratory combustion of carbon-compounds is traceable back to that stored in the form of potential energy of chemical combination in carbohydrates, which were formed by the help of the sun's rays in assimilation (cf. p. 216). Energy is not only liberated in the more or less complete combustion of carbon-compounds but may be obtained in other chemical processes. While most plants consume organic substances in respiration, some lower plants, especially Bacteria, depend on energy obtained from other chemical changes. Thus sulphur-bacteria oxidise sulphuretted hydrogen to sulphur, and this in turn to sulphuric acid ; others, according to NATHANSOHN, oxidise thio-sulphates. The nitrite-bacteria form nitrous acid from ammonia and amides, while nitrate-bacteria convert the nitrous into nitric acid. It is doubtful whether the iron-bacteria gain a similar benefit from the oxidation of compounds of iron. The energy obtained in such processes may serve to replace the driving power of respiration, or, as has been shown for the nitro-bacteria (p. 189), and is possibly the case for the sulphur-bacteria also, may effect the synthesis of organic carbon-compounds. The working power is thus devoted to one or other process of the life of the plant (59).

Fermentation and Respiration (60).—In the section on special modes of nutrition it was stated that when this is effected at the expense of organic food material, fermentation is frequently set up in the substratum. Since fermentation is a process of decomposition associated with a liberation of energy stored in organic compounds, it may be serviceable in the same way as respiration. Its amount may also be more or less influenced by the respiratory needs of the organism.

Thus, when the yeast plant is living as an anaerobe, the greater part of the organic substratum (about 98-99 per cent) is fermented. When growing as an aerobe, with a full supply of oxygen, a larger amount of the substratum is available for use in the processes of growth and multiplication.

Since, even in the latter case, a large part of the grape-sugar (according to BUCHNER and RAPP about 85 per cent) is fermented, it may be concluded that the process of fermentation, though under certain circumstances a source of energy to the plant, is to some extent independent of the respiratory needs of the latter, and may have a further significance. Since the products of fermentation are as a rule far better endured by the organisms which have given rise to them than by others, their production may have an œcological value in the struggle with competing organisms. Oxygen-respiration is also to a certain extent independent of the other vital manifestations. It is most active at a temperature a little below that which causes the death of the organism, when all other activities are being arrested by the heat.

Heat produced by Respiration.—Respiration is, chemically and physically considered, a process of oxidation or combustion, and, like them, is accompanied by an evolution of heat. That this evolution of heat by plants is not perceptible is due to the fact that considerable quantities of heat are rendered latent by transpiration, so that transpiring plants are usually cooler than their environment ; and also to the fact that plants possess very large radiating surfaces in proportion to their mass.

The spontaneous evolution of heat is easily shown experimentally, if transpiration and the loss of heat by radiation are prevented and vigorously respiring plants are selected. Germinating seeds (Peas), if examined in large quantities, show under proper conditions a rise in temperature of 2° C. The greatest spontaneous evolution of heat manifested by plants has been observed in the inflorescence of the Araceae, in which the temperature was increased by energetic respiration 10°, 15°, and even 20° C. Also in the large flower of the *Victoria regia* temperature variations of 15° C. have been shown to be due to respiration. One gramme of the spadix substance of an Aroid exhales, in one hour, up to 30 cubic centimetres CO_2 ; and half of the dry substance (the reserve sugar and starch) may be consumed in a few hours as the result of such vigorous respiration. In the process of wound-healing in plants a noticeable rise in temperature also occurs.

That other processes, in addition to respiration, co-operate in the production of heat is apparent from the fact that the amount of heat evolved does not vary proportionally to the carbonic acid exhaled.

The Movement of Gases in Respiration

In plants of simple construction the cells which are in direct contact with the air or water can absorb the requisite oxygen directly ; while cells in the midst of tissues are dependent upon the oxygen which can diffuse through the surrounding cells. Such a diffusion from cell to cell would not, however, be adequate, in the case of the large cellular bodies of the higher plants, to provide the living cells of the interior with a sufficient supply of oxygen. This is accomplished by means of the air-spaces, which, as INTERCELLULAR PASSAGES, penetrate the tissues in all directions and so bring to the protoplasm of the inner cells the air entering through the STOMATA and LENTICELS. The path of the respiratory gases is thus the same as that followed by the gases in transpiration and assimilation (pp. 205, 221).

The movement of the gases within the intercellular spaces is due partly to the diffusion, induced by the constant interchange of gases caused by respiration, assimilation, and transpiration, and partly to movements in mass arising chiefly from modifications of the temperature, pressure and moisture of the surrounding atmosphere, but also increased by the movement of the plants themselves, through the action of the wind.

That the intercellular spaces were in direct communication with each other and also with the outer atmosphere was rendered highly probable from anatomical investigation, and has been positively demonstrated by physiological experiment. It is, in fact, possible to show that air forced by moderate pressure into the intercellular passages makes its escape through the stomata and lenticels; and conversely, air which could enter only through the stomata and lenticels can be drawn out of the intercellular passages. The method of conducting this experiment can be seen from the adjoining figure (Fig. 212).

Intercellular air-spaces are extensively developed in water and marsh plants, and occupy the greater part of the floating portions of the plant. The submerged portions of water plants unprovided with stomata thus secure a special internal atmosphere of their own, with which their cells maintain an active interchange of gases. This internal atmosphere is in turn replenished by slow diffusion with the gases of the surrounding medium. In marsh-plants, which stand partly in the air, the large intercellular spaces form connecting canals through which the atmospheric oxygen without being completely used up can reach the organs growing deep in the swampy soil and cut off from other supplies of oxygen. In some cases the need of a supply of oxygen to such roots is met by specialised roots (pneumatophores) which project vertically from the muddy soil (Fig. 213).

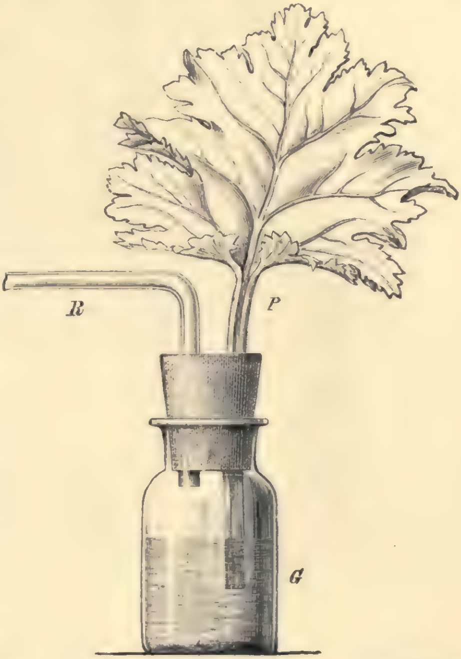


FIG. 212.—Experiment to show the direct communication of the external atmosphere with the internal tissues of plants. The glass tube *R*, and the leaf *P*, are fitted airtight in the bottle *G*; upon withdrawal of the air in the bottle by suction on the tube *R*, the external air penetrates the intercellular spaces of the leaf, through the stomata, and escapes in the form of small air-bubbles from the cut surface of the leaf-petiole. (From DETMER'S *Physiol. Prakt.*)

Phosphorescence. — Under the same conditions as the respiratory process a limited number of plants, particularly Fungi and Bacteria, emit a phosphorescent light. This phosphorescence at once disappears in an atmosphere devoid of oxygen, only to reappear on the admission of free oxygen. On this account the phosphorescent Bacteria, according to BEYERINCK, afford a delicate test for the activity of assimilation. All the circumstances which facilitate respiration intensify phosphorescence; the converse of this is also true. According to the results of investigations concerning the phosphorescence of animals, from which that of plants does not probably differ in principle, the phosphorescence is not directly dependent upon the respiratory processes.

The best-known phosphorescent plants are certain forms of Bacteria which occur in the sea and the mycelium, formerly described as "Rhizomorpha," of the Fungus *Agaricus melleus*. As further examples of spontaneously luminous Fungi may be cited *Agaricus olearius*, found growing at the foot of olive trees in South Europe, *Polyporus sulphureus* and other less familiar Agarics (*Ag. igneus*, *noctilucens*, *Gardneri*, *Mycena illuminans*, etc.). The phosphorescence of decaying wood is also, without doubt, due to the growth of Fungi or Bacteria, but sometimes to an insect (*Neanura*) which reacts in this way when disturbed. On phosphorescent fish or meat harmless phosphorescent Bacteria (*Microspira photogena*, *Pseudomonas lucifera*) occur. According to MOLISCH *Micrococcus phosphoreus* usually occurs on meat which has been moistened with a 3 per cent solution of common salt and kept at a low temperature. Of plants taking part in the phosphorescence seen in the sea, the most important are *Pyrocystis noctiluca* belonging to the Gymnodiniaceae and certain Peridineae. Their phosphorescence, according to observations on *Ceratium tripos* made by REINKE, is brought about by mechanical as well as by thermal and chemical stimuli.

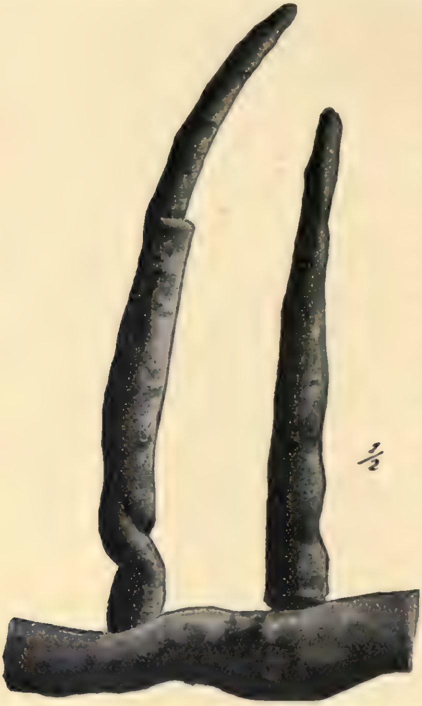


FIG. 213.—Respiratory root of *Avicennia*, one of the Mangroves. (½ nat. size ; from SCHIMPER's *Plant-Geography*.)

The so-called phosphorescence of the Moss *Schistostega*, of the Flagellate *Chromophyton Rosanoffii*, and of some

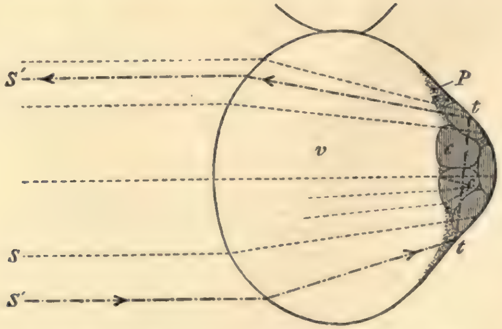


FIG. 214.—Phosphorescent cell of the protonema of *Schistostega*. *S′ S′*, Path of a ray of light which after passing through the chloroplasts acquires a green tinge and is totally reflected. (Cf. Fig. 172.)

Selaginellas and Ferns, has nothing in common with actual phosphorescence, but is produced solely by the reflection of the daylight from peculiarly formed cells (Fig. 214). The phosphorescence observed in some seaweeds results, on the other hand, from the fluorescence and opalescence of certain of their albuminous substances, or from the iridescence of their cuticular layers ([61]).

The light occasionally emitted by some floral structures on sultry nights is, we must assume, electrical and comparable to St. Elmo's fire.

IV. Growth

The size which plants may attain varies enormously. A Mushroom seems immeasurably large in contrast with a *Micrococcus*, but small if compared with a lofty Californian *Sequoia*. A *Bacillus* of the size of a Mushroom, or a Mould-Fungus of the height of a *Sequoia*, are, with their given organisation, physiologically as inconceivable as a Mushroom with the minuteness of a *Micrococcus*. The size of an organism accordingly is an expression of its distinct individuality, and stands in the closest relation to structure and conditions of life, and in the individuals of a species only varies within certain narrow limits.

However large a plant may be, and however numerous its cells, it nevertheless began its existence as a single cell, microscopically small and of the simplest structure. To attain its final size and perfect development it must grow, that is, it must enlarge its body and undergo differentiation. Even for the minute unicellular Bacteria growth is essential, as they multiply chiefly by cell division. Each daughter cell must grow and attain the dimensions of the parent cell, or in a few generations the capacity for existence itself will be lost through their continually decreasing size. It is in fact impossible to conceive of a plant where development is not the result of growth. If a growing Oak or Cedar be compared with the single spherical egg-cell from which it has arisen, it is at once clear that by the term growth we mean not only an increase in volume, but include also a long series of various developmental stages, and external and internal modifications. A mere increase in volume does not necessarily imply growth, for no one would say that a dried and shrivelled turnip grows when it swells in water. On the contrary, active growth may be accompanied by a considerable loss of substance, as is shown by the sprouting of potatoes kept in a dark cellar; water is lost through transpiration as well as organic substance through respiration, and yet the new shoots show true growth.

In the lower organisms growth is exhibited in its most simple form. In an amœba or a plasmodium growth is simply an increase in their substance; in a unicellular Alga or in a Fungus it means, in addition to this, an enlargement of their cell walls. In the higher plants the processes of growth are far more complicated and various, so that, according to SACHS, three chief phases of growth can be distinguished, which, however, are not sharply separated, but merge imperceptibly one into the other :—

1. The embryonic phase in which the rudiments of new organs are formed.

2. The phase of elongation of the already formed embryonal organs.

3. The phase of internal development and completion of the tissues.

The Embryonal Development of the Organs

Plants, in contrast to the higher animals, continually develop new organs. These arise either from tissues retained in their embryonic condition, as at the growing point, or they have their origin in regions which have already more or less completely attained their definite form. The leaves and shoots spring directly from the tissues of the growing point; the first lateral roots, however, make their appearance at some distance from the growing point, where a perceptible differentiation of the tissues has already taken place.

Leafy shoots may also take their origin from old and fully developed tissues, which again assume an embryonic character, accompanied by an accumulation of protoplasm and renewed activity in cell division. But as this only occurs in exceptional cases, shoots which thus arise out of their regular order are termed ADVENTITIOUS.

The manner of the **Formation of New Organs at the Growing Point** has already been described in the morphological portion of this book. It is only necessary here to again call attention to the fact that the young organs, with few exceptions, develop in acropetal succession, so that the youngest is always nearest the apex. The point from which new organs arise, and the number which develop, are chiefly dependent upon inherited internal disposition. External factors can, however, exert an effect in particular cases. The influence of such factors as light, gravity, chemical and mechanical stimuli, which at certain times in the later life of the tissues is of extreme importance, has usually but little effect on the embryonal development. Yet, on the other hand, the position of the first division wall of the germinating spore of *Marsilia* is determined by the action of gravity, and the direction of the first wall (as well as of the preceding nuclear division) in the spore of *Equisetum* and the ova of *Cystoseira barbata*, *Pelvetia*, *Haliseris*, and *Ascophyllum* among the Fucaceae, and of *Dictyota* is determined by its relative position to the light (^{62}).

In **Adventitious Formations**, on the contrary, the influence of external forces is often very evident, as, for example, in the formation of climbing-roots, which in the Ivy and other root-climbers are developed only on the shaded side of the stem. In the Alga *Caulerpa* the new leaf-like organs arise only on the illuminated side of the parent organ. It is, on the other hand, the force of gravity which excites the formation of roots on the under side of underground rhizomes. It is also due to gravity that the growing points of shoots are formed only from the upper side of the tubers of *Thladiantha dubia*, or that new twigs develop, for the most part, from the upper side of the obliquely growing branches of trees. Contact stimuli, on the other hand, determine the primary inception and point of development of the haustoria of *Cuscuta*. The sexual organs of Fern prothallia are always developed on the side away from the light; that is, in normal conditions on the under side, but in case of artificial illumination on the upper side.

As a result of one-sided illumination and the stimulus of gravity, together with the favouring influence of moisture, the rhizoids spring only from the under side of the gemmæ of *Marchantia*, so that eventually the two originally similar sides assume an altogether different anatomical structure.

Many adventitious formations are the result of definite external causes; as, for example, the galls induced by the stings of insects and the deposits of animal eggs and larvæ (cf. p. 165).

The development of adventitious formations is especially induced by MUTILATION of plants; the same effect may result when the organs or growing points though uninjured become functionless. NEW FORMATIONS are in this manner produced at points from which they would never have arisen on the uninjured plants. In the case of Pelargoniums, Willows, and many other plants, it is possible to induce the formation of roots wherever the shoots are cut. In other plants, however, there seem to be certain preferred places, such as the older nodes, from which, under the same circumstances, roots develop. In like manner new shoots will appear in the place of others that have been removed. IN THE DEVELOPMENT OF NEW FORMATIONS ON A MUTILATED PLANT THOSE VERY ORGANS ARISE, OF WHICH THE PLANT HAS BEEN DEPRIVED. Root-less shoots develop first of all new roots. Roots and root-stocks deprived of their shoots form first new shoots. In these processes there is manifested an internal reciprocity in the formative growth of organs, which has been termed the CORRELATION OF GROWTH.

Correlation of growth is often, also, very apparent in the normal development of the organs of uninjured plants. It is due to this that scales of buds are developed in their special form rather than as foliage leaves. For, as GOEBEL showed, it is possible by artificial means, as, for example, by the timely removal of the leaves of the parent shoot of *Aesculus*, *Acer*, *Syringa*, *Quercus*, or in the case of *Prunus Padus*, by cutting off the upper extremity of the shoots, to induce the formation of normal foliage leaves in the place of the scales. The vigorous growth which ensues in the fruit and in the fruit-coverings after fertilisation and development of the embryo in the ovule, affords another example of correlation; for, in case no fertilisation of the egg-cell occurs, all those changes which produce a ripe fruit from the flower do not take place; and, instead, another correlative process is manifested by which the now useless organs are discarded. Certain plants, especially those modified by cultivation, form an exception to this: in many varieties of Banana, in the seedless Mandarin, and in the variety of raisins known as Sultana, etc., although no seeds capable of germination are produced, the formation of a fruit is nevertheless continued. Even in these instances it is essential for the formation of fruit that there shall have occurred a previous pollination of the stigma, or the fertilisation of the ovules, which, however, do not mature. According to MULLER THURGAU (^{63}) the formation of seeds in grapes exerts an influence on the form, quantity, and quality of the succulent portion of the berry. In some few exceptional cases, however, as in the fruits of the Fig and Gherkin and the seeds of Cycads, even this impetus to fruit formation is not necessary. The manner of the formation of conducting tissues in plants, and also their anatomical development, are regulated by correlation. From these few instances it may be seen how the principle of correlation affects the most various of the vital processes, even under normal conditions, and how the harmonious development and function of the single members of the plant body are controlled by it.

The polarity manifested by plants should also be considered as a special example of the correlation existing between the different parts of the plant body. This polarity is particularly apparent in stems and roots, and finds its expression in the tendency of every small piece of a stem to develop new shoots from that end which was nearer the stem apex, while the roots take their rise from the other end. Pieces of roots in like manner send out roots from the end originally nearer their apex, and shoots from the end towards the stem.

In accordance with this principle, detached pieces of stems produce new shoots from their "shoot-pole," and injured roots new roots from their "root-pole." This polarity, particularly investigated by VÖCHTING and SACHS, is supplemented according to GOEBEL by the nutritive current setting towards the wounded surface; it makes itself apparent in even the smallest pieces of stems or roots, and may, in this respect, be compared to the magnetic polarity exhibited by every small piece of a magnet. Unlike poles of a plant may readily be induced to grow together, while like poles may only be brought to do so with difficulty, and then do not develop vigorously. As a result of such experiments, a radial polarity has also been recognised by VÖCHTING in stem and root tissue: thus, for instance, pieces of a stem or root, inserted in a lateral incision of a similar organ, become united with it, if they are so placed that the side originally outermost occupies the same relative position in the new organ, but if this position is altered no such union takes place. Leaves take, in respect to polarity, a special position, for they are not organically included within new formations derived from them. Thus, from the basal end of a leaf, an entire plant, with roots, stem, and leaves, may arise, while the regenerative leaf itself gradually dies. It is of especial interest to observe the effect of external influences upon the position of new formations, when they come into opposition to the internal disposition of the plants themselves. In this respect, the behaviour of different species varies greatly. In one, the internal factors predominate, that is, the new formations appear quite independently of external conditions; in another, the external influences for the moment prevail, but the internal disposition of the plant, when thus constrained for the time being, ultimately makes itself apparent and the new formations never develop vigorously. A willow twig, planted in a reversed position, with the shoot-pole in the ground, will produce roots, and from the root-pole may even produce shoots. These, however, usually soon die and their place is supplied by other stronger shoots arising from the shoot axis just above the roots. It is only by the most careful suppression of any such developments that the shoots from the root-poles may be kept alive. In the trailing shoots of such plants as the Blackberry roots may be formed beneath the uninjured growing point. In so-called "weeping" trees, the formation of side branches from the upper side of the hanging branches is favoured by external conditions, but the internal polarity prevents their vigorous development, and those formed soon die. In the cultivation of vines and fruit trees this peculiarity is utilised to produce short-lived, fruit-producing shoots by bending over the vines or training the branches of the trees in the cultivation of wall fruits. On the other hand, in some cases the internal polarity is easily overcome by external influences. It is sometimes sufficient merely to reverse the erect thallus of *Bryopsis*, one of the Siphoneae, to convert the former apical portion into a root-like tube which penetrates the substratum and fastens itself to the grains of sand. It has also been positively determined, although otherwise such cases are unknown among the higher plants, that the growing points of the roots of *Neottia* and of certain Ferns (*Platycerium*, *Asplenium esculentum*) may be converted through some inherent tendency into the vegetative cone of a stem (cf. p. 47) (64).

The correlation phenomena manifested in the formation of new organs have the greatest practical importance, for the propagation of plants by cuttings or grafting is based upon them.

In artificial reproduction detached pieces of plants are made use of for the purpose of producing a fresh complete plant. In many cases this is easily done, but in others it is more difficult or even impossible. The favourite and easiest method is by means of CUTTINGS, that is, the planting of cut branches in water, sand, or earth, in which they take root (Pelargonia, Tradescantias, Fuchsias, Willows, etc.). Many plants may be propagated from even a single leaf or portion of a leaf, as, for instance, is usually the case with Begonias. In other cases the leaves, while still on the parent plant, have the power to produce adventitious buds, and, in this way, give rise to new plants (see Vegetative Reproduction). Even from roots or pieces of roots it is also possible to propagate some few plants. An example of this is afforded by *Ipecacuanha*, whose roots are cut in pieces and then sown like seeds. The Dandelion possesses the same capability of developing from small portions of the root, and to this peculiarity is due the difficulty with which it is destroyed.

In GRAFTING or BUDDING, cuttings from one plant are inserted in another, so that they grow together to form physiologically one plant. The two parts stand in correlation to one another, for a twig, which if planted in the soil would have developed roots, when grafted on another plant forms no roots but enters into an intimate relation with the stock. It adopts the roots of the latter and its buds may be said to be adopted by the stock and no new organs are formed. When the affinity between graft and stock is a distant one, it appears from LINDEMUTH's observations that roots may be formed from the graft even in the air. The union is accomplished by means of a callus (p. 151), formed by both the scion and the adopted stock. Vessels and sieve-tubes afterwards develop in the callus, and so join together the similarly functioning elements of both parts. Such an organic union is only possible between very nearly related plants, thus, for example, of the Amygdalaceae, the Plum, Peach, Almond, Apricot, may readily be grafted one upon the other, or of the Pomaceae, the Apple with the Quince; but not the Apple with the Plum, nor (as has been asserted) with the Oak.

In spite of the physiological union between the old stock and the newly formed growth, from a morphological standpoint they lead an altogether separate and distinct existence. They may, however, exert an influence on each other; thus annual plants grafted on biennial or perennial stocks attain an extended period of existence. In its structural character, forms of tissues, mode of secondary growth, formation of bark, etc., each maintains its own individuality. In special cases it has been affirmed that they do mutually exert, morphologically, a modifying effect upon each other (graft-hybrids). This could only result from fusion of the protoplasts of stock and graft in the callus (Fig. 247).

In practice several different methods of inserting grafts are in use, but only the more important can be mentioned here. **Grafting** is the union of a shoot with a young and approximately equally-developed wild stock. Both are cut obliquely with a clean surface, placed together, and the junction protected from the entrance of water and fungi by means of grafting wax (Fig. 215, *II.*). Cleft or tongue grafting is the insertion of weaker shoots in a stronger stock. Several shoots are usually placed in the cut stem of the stock, care being taken that the cambial region of the different portions are in contact, that the cortex of the shoots is in contact with that of the stock. In other methods of grafting the cut end of the shoot is split longitudinally and the cut shoot inserted in the periphery, or a graft may be inserted in the cortex or in the side of the stock. In grafting in the cortex the flatly-cut shoot is inserted in the space cut between the bark and the splint wood (Fig. 215, *I.*). In lateral grafting, the shoot, after being cut down, is wedged into a lateral incision in the stock.

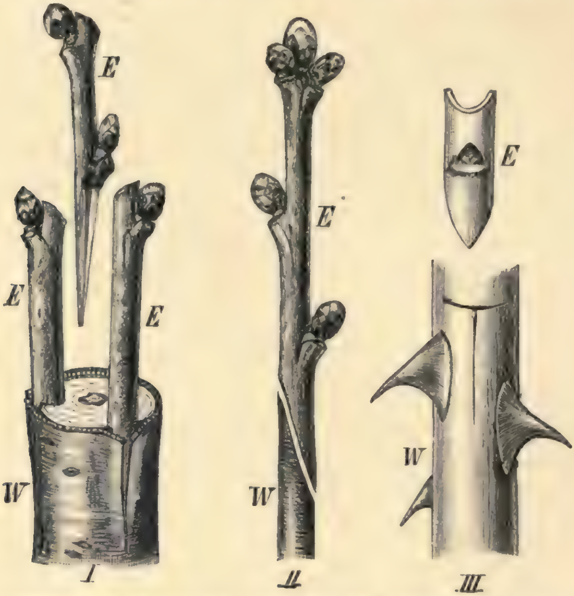


FIG. 215.—Different modes of grafting; *I*, Crown grafting; *II*, splice grafting; *III*, bud grafting; *W*, stock; *E*, scion.

A special kind of grafting is known as BUDDING (Fig. 215, *III.*). In this process a bud ("eye") and not a twig is inserted under the bark of the stock. The "eye" is left attached to a shield-shaped piece of bark, which is easily separated from the wood when the plants contain sap. The bark of the stock is opened by a T-shaped cut, the "eye" inserted, and the whole tightly covered. Occasionally some of the wood may be detached with the shield-shaped piece of bark (budding with a woody shield). In the case of sprouting buds, the budding is made in spring ; in dormant buds, which will sprout next year, in summer.

The Phase of Elongation

For the performance of their proper functions, the embryonic rudiments of the organs must unfold and enlarge and assume their characteristic appearance. This subsequent enlargement of the embryonic organs of plants is accomplished in a peculiar and economical manner. While the organs of animals increase in size only by a corresponding increase of organic constructive material and by the formation of new cells rich in protoplasm, and thus require for their growth large supplies of food substance, plants attain the chief part of their enlargement by the absorption of water—that is, by the incorporation of an inorganic substance which is most abundantly supplied to them from without, and to obtain which no internal nutritive processes are first necessary.

The absorption of water by living cells does not take place with the same rapidity and without interruption as in the case of porous bodies. Before the cells can take up additional water they must enlarge by actual processes of growth. The water, penetrating the young cells by imbibition or by the force of osmotic pressure, is uniformly distributed through the protoplasm, which fills the cell ; when the protoplasm is already abundantly supplied with water, it is accumulated in vacuoles (Fig. 58). As the vacuoles contain also organic and inorganic matter in solution, they exert an attractive force and give rise to further absorption of water. The sap of the vacuoles would, in turn, soon be diluted and its attractive force diminished, were it not that the regulative activity of the protoplasm soon provides for a corresponding increase of the dissolved salts, so that the concentration and attractive force of the sap are continually being restored or even increased. The separate vacuoles thus enlarged ultimately flow together into one large sap-cavity in the middle of the cell.

In this process the volume of the cell may increase a hundred-fold (in the internodal cells of the Characeae two thousand-fold) without any marked increase in the amount of protoplasm. The enlargement of the cell has been almost wholly produced by the increased volume of water in the sap cavity, which, to distinguish it from the "nutrient water," "imbibition water," and "constitution water" of the plant, may be designated "distension water."

As is observed in a whole series of vital phenomena, the rate of distension of the walls with the distension water is not uniform, but BEGINS SLOWLY, INCREASES TO A MAXIMUM RAPIDITY, AND THEN, GRADUALLY DIMINISHING, ALTOGETHER CEASES. As all the cells of equal age in an organ go through this process of distension at the same time, the phenomena of increase and decrease in the rate of growth are apparent in the growth of the organ, and give rise to GRAND PERIODS OF GROWTH. Minor periods, or fluctuations in the rate of growth, occurring within the grand periods, are due to irregularities in the swelling of the cells, occasioned by change of temperature, light, and other influences operative on growth, while the causes of other abrupt changes in the rate of growth are still unknown (65).

The large amount of water absorbed by the growing organ in the process of elongation does not lessen its rigidity, but, on the contrary, it is to the turgor thus maintained that the rigidity is due (cf. p. 178). Osmotic pressure seems also to take an important part in the growth of the cell wall itself. Cells in which the turgor is destroyed by a decrease in the water-supply exhibit no growth of their cell walls ; it is thus evident that the distension of the cell walls is physically essential for their surface-growth. This distension is in itself, however, by no means the cause of their growth ; the internal physiological conditions of the growth of the cell walls are dependent upon the activity of the living protoplasm. Without the concurrent action of the protoplasm, there is no growth in even the most distended cell wall ; on the other hand, active growth of the cell wall may take place with the existence of only a small degree of turgor tension. A correspondence between the turgor tension of the cell walls and the amount of growth cannot under these conditions be expected, nor can, on the other hand, the conclusion be drawn that turgor tension is inoperative in the processes of growth. The importance of the turgor tension is variously estimated, according to whether the growth of the cell wall is regarded as resulting from the interpolation of new particles of constructive material between the already existing particles of the cell wall substance (INTUSSUSCEPTION) or to the plastic (*i.e.* inelastic, not resuming its original position) expansion of the distended cell wall. In the latter case the growing membrane would continually become thinner, and require to be strengthened by the deposition of new layers upon it (APPOSITION). Both processes, which may occur together, probably take part in the growth of cell walls. The necessity of a certain amount of turgor, if growth is to result from plastic stretching, is self-evident ; the stretching of the wall by the internal tension, though facilitating the introduction of the new particles in growth by intussusception, is, however, not so indispensable in this case.

The assumption of a growth by intussusception is intimately related to the views held on the finer (or so-called molecular) structure of organic substances. The power of swelling in water, which may even lead to complete solution, exhibited by organic substances, shows that the water of imbibition does not merely penetrate into pre-existing capillary spaces, but makes a passage for itself by separating the solid particles from one another. It is further evident that these particles must be of minute (molecular) size. The intimate penetration of the water is the expression of a powerful molecular attraction, which is capable of exerting an enormous force ; it is rendered possible by the peculiar molecular construction of organic substances, the cohesion of which is only gradually overcome by the water present in excess. The arrangement of the particles has been pictured as resembling a network or a honeycomb, while the frequent occurrence of double refraction as an optical property of organic substances has been explained as due to the crystalline structure and definite arrangement of the groups of molecules (micellæ of NAEGELI) or to the relations of tension in a colloidal honeycomb-like system (BÜTSCHLI). The new cellulose particles would penetrate into the cell membrane, as particles of colouring matter may be introduced with the imbibition water into a colloid organic substance (66).

The process of elongation has so far been considered only in relation to the single cell, preparatory to the consideration of the phenomena presented by the growth of multicellular organs. With regard to this it is to be noted that the intensity of growth in two organs of equal total growth is greater the shorter the growing zone is. BUCHNER observed in fungal hyphæ and pollen tubes in which growth is restricted to just behind the apex that its amount per unit of time was 220 per cent as compared with ½-1 per cent in the majority of the higher plants.

The operations of growth in plant organs proceed very slowly; so slowly as to be, in general, imperceptible. Only some fungal hyphæ and the stamens of many Gramineae grow so rapidly that their elongation is evident, even to the naked eye. The hyphæ of *Dictyophora* grow in length to the extent of 5 mm. per minute (A. MÖLLER) and according to ASKENASY, an increase in length of 1·8 mm. a minute has been observed in the stamens of *Triticum* (Wheat). This approximately corresponds to the rate of movement of the minute-hand of a watch. In comparison with these, the next known most rapidly growing organ is the leaf-sheath of the Banana, which shows an elongation of 1·1 mm., and a Bamboo shoot, an increase in length of 0·6 mm. per minute; a strong shoot of *Cucurbita* grows 0·09-0·1 mm. per minute, while most other plants, even under favourable circumstances, attain but a small rate of elongation (0·005 mm. and less per minute) (67).

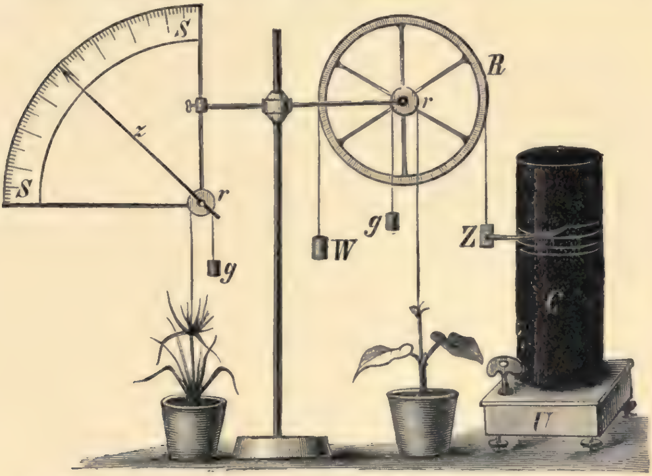


FIG. 216.—Simple and self-registering auxanometer. For description see text.

In order to measure the growth in length of a plant, it is customary to magnify in some way the actual elongation for more convenient observation. This may be effected by means of a microscope, which magnifies the rate of growth correspondingly with the distance grown. For large objects, the most convenient and usual method of determining the rate of growth is by means of an AUXANOMETER. The principle of all auxanometers, however they may differ in construction, is the same, and is based upon the magnification of the rate of growth by means of a lever with a long and short arm. In Fig. 216, at the left, a simple form of auxanometer is shown. The thread fastened to the top of the plant to be observed is passed over the movable pulley (*r*), and held taut by the weight (*g*), which should not be so heavy as to exert any strain on the plant. To the pulley there is attached a slender pointer (*Z*), which is twenty times as long as the radius of the pulley, and this indicates on the scale (*S*) the rapidity of the growth, magnified twenty-fold. By a growth in the length of the plant-stem of ⅕ mm., the pointer would accordingly register 4 mm.

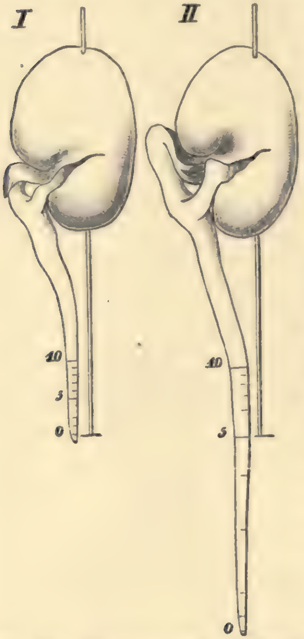


FIG. 217.—Unequal growth of different regions of the root-tip of *Vicia Faba*. *I*, The root-tip divided by marking with india-ink into 10 zones, each 1 mm. long. *II*, The same root after twenty-two hours; by the unequal growth of the different zones the lines have become separated by unequal distances. (After SACHS.)

Self-registering auxanometers are also used, especially in making extended observations. In Fig. 216, at the right, is shown one of simple construction. The radius of the wheel (*R*) corresponds to the long arm, and the radius of the small wheel (*r*) to the short arm of the lever, in the preceding apparatus. Any movement of the wheel, induced by the elongation of the shoot, and the consequent descent of the weight (*G*), is recorded on the revolving drum (*C*) by the pointer attached to the weight (*Z*), which is, in turn, balanced by the counterweight (*W*). The drum is covered with smoked paper, and kept in rotation by the clock-work (*U*). If the drum is set so that it rotates on its axis once every hour, the perpendicular distances between the tracings on the drum will indicate the proportional hourly growth.

The grand periods in the growth of an organ, due to the internal causes, are clearly shown by such self-registering auxanometers by the gradual increase and final decrease in the perpendicular distances representing the increment of growth. STREHL found the daily growth in length of a root of Lupine, expressed in tenths of millimetres, to be: 58, 70, 92, 97, 165, **192**, 158, 137, 122, 83, 91, 59, 25, 25, 8, 2, 0. For the first internode of the stem, growing in the dark, the daily growth observed was: 8, 9, 11, 12, 35, 43, 41, 50, 51, 52, **65**, 54, 43, 37, 28, 18, 6, 2, 0.

The grand periods of growth, that is, the gradual increase from zero to a maximum, and the succeeding decrease to zero again, are, however, not evident throughout the whole of a root; during the growth in length only a small portion of a root is actually, at one time, in process of elongation. In roots of land plants the growing region extends over only about one centimetre of the extreme tip, often indeed over only ½ centimetre, while all the rest of the root has already completed its growth in length. The length of the growing region is influenced by such external conditions as mechanical hindrance, cold, warmth, dryness, etc., and exhibits consequent variations. That the grand period is exhibited by this short growing region may be made clear by marking off with india-ink, near the tip of a root, narrow zones of equal width, which would thus also be made up of cells of nearly equal size. In Fig. 217 *I*, is shown a germinating Bean (*Vicia Faba*), whose root-tip has been marked in this way; Fig. 217 *II*, represents the same root after twenty-two hours of growth. The marks have become separated by the elongation of the different zones, but in different degrees, according to their position. The greatest elongation is shown by the transverse zone 3; from there the growth in length decreases towards the younger zones (2 and 1), as well as towards the older (4 to 10). This peculiar distribution of growth is but the result of the grand periods of growth of the cells in zones of different ages (68). In the millimetre-broad zones of a root of *Vicia Faba* SACHS found, after twenty-four hours, that the increase in growth, expressed in tenth-millimetres, was as follows:—

Zones:	I.,	II.,	III.,	IV.,	V.,	VI.,	VII.,	VIII.,	IX.,	X.,	XI.
Increase:	15,	58,	**82**,	35,	16,	13,	5,	3,	2,	1,	0.

The elongating region in shoot axes is generally much longer than in roots, and usually extends over several centimetres, in special cases even over 50 or more centimetres. The distribution of the increase corresponds in stems, as in roots, with the grand periods of growth of the cells. Even by INTERCALARY GROWTH, where the region of elongation is not confined to the apex but occurs in any part of the organ, generally at its base (leaves and flower-stalks of many Monocotyledons), grand periods of growth are also apparent. A shoot of *Phaseolus multiflorus* which was divided, from the tip downwards, into transverse zones 3·5 mm. broad, showed in forty hours, according to SACHS,

in zones:	I.,	II.,	III.,	IV.,	V.,	VI.,	VII.,	VIII.,	IX.,	X.,	XI.,	XII.
an increase of	20,	25,	45,	**65**,	55,	30,	18,	10,	10,	5,	5,	5

tenth-millimetres.

This periodicity in the growth in length occurs even when the external influences affecting growth remain constant, and is determined by internal causes alone.

Distinct periods of growth separated by an interval of time occur, according to MIYAKE, in the scapes of the Dandelion, the first period in relation to the development of the flowers, the second to that of the fruits. A similar behaviour is found in other organs whose function after a time becomes altered (flower or fruit stalks in *Linaria cymbalaria*, and *Arachis hypogaea* (p. 285), and floral envelopes which later protect the fruits in other cases).

External Influences upon Growth (69).—External factors often take an active part in the process of elongation, either as retarding or accelerating influences. As growth is itself a vital action, it is affected by any stimulus acting upon the protoplasm; on the other hand, as it is also a physical function, it is modified by purely physical influences. Growth is particularly dependent upon temperature, light, moisture, the supply of oxygen and other substances, and the existence of internal pressure and tension. It is also influenced by injuries.

The INFLUENCE OF TEMPERATURE is manifested by the complete cessation of growth at a temperature less than 0° or higher than 40°-50°. Between the MINIMUM and MAXIMUM temperatures, at which growth ceases, there lies an OPTIMUM temperature (p. 176), at which the rate of growth is greatest. This optimum temperature usually lies between 22° and 37° C. The three CARDINAL POINTS OF TEMPERATURE here given include a wide range, as they vary for different species and even for individual plants of the same species, and for their several vital processes. In tropical plants the minimum temperature may be as high as + 10° C., while those of higher latitudes, where the first plants of spring often grow through a covering of snow, as well as those of the higher Alps and polar regions, grow vigorously at a temperature but little above zero. In like manner, the optimum and maximum temperatures show great variation in different species of plants. Thus some Algae and Bacteria grow in hot springs at a temperature of 80° C., which would be at once fatal to other plants. The optimum does not usually lie in the middle between the minimum and maximum, but is nearer the maximum. (On the dependence of the cardinal points on external conditions cf. p. 176.)

A certain amount of variation in the temperature favours the germination of seeds and the unfolding of young shoots more than exposure to any constant temperature. This is due to the optima for the different processes concerned lying at different temperatures (70).

The INFLUENCE OF LIGHT makes itself felt in a different manner from changes of temperature. Light as a general rule retards growth. This is apparent from observations on stems and roots grown in the dark, and is also true in regard to the growth of leaves, if the disturbing effects resulting from long-continued darkness be disregarded. Too great an intensity of light causes a cessation of the growth of an organ, while feeble illumination or darkness increases it. The effect of darkness upon the growth of plants is, however, differently manifested according to its duration, whether it be continuous, or interrupted, as in the changes of night and day. Long-continued darkness produces an abnormal growth, in that the growth of certain organs is unduly favoured, and of others greatly retarded, so that a plant grown altogether in the dark presents an abnormal appearance. The stems of Dicotyledons, in such case, become unusually elongated, also soft and white in colour. The leaf-blades are small and of a bright yellow colour, and remain for a long time folded in the bud (Fig. 218, *E*). A plant grown under such conditions is spoken of as "etiolated."

This diminution in the size of the leaf-blades and the elongation of the stem (and leaf-stalks) are not manifested by all plants, nor under all circumstances. The stems, for instance, of certain *Cacti* are much shorter when grown in the dark than in the light, and their flattened shoots remain cylindrical. Similarly, the leaves of varieties of the Beet (*Beta*) grow as large, or even larger, in the dark than in the light; this is also true, under conditions favourable to nutrition, of the leaves of other plants (*Cucurbita*). In the shade of a forest leaves often become larger than in full daylight. They are then proportionally thinner, and the palisade cells which, in leaves fully exposed to the light, are in close contact, become pointed below, and thus leave large intercellular spaces between them. In this way the modifying influence of light of diminished intensity is apparent in the internal structure of such shade-leaves. Flowers, however, if sufficient constructive material be provided by the assimilating leaves, develop, according to SACHS' observations, as well in the dark as in the sunlight, except that they are sometimes paler in colour. If, however, the assimilatory activity of the green leaves be reduced or destroyed by depriving them of light, many plants, as VÖCHTING found, form only inconspicuous or cleistogamous flowers; as GOEBEL shows, the same result may follow when the nutrition of the flowers is interfered with by poor soil or the excessive development of the vegetative organs.

The tissues of etiolated stems and leaf-stalks are richer in water and thinner-walled than in normally growing plants. Even the roots of such plants are often found to be less strongly developed. The supply of reserve material at the disposal of plants growing in the dark is utilised, with the assistance of an unusual amount of distension water, in the elongation of the axis. This elongation of the shoot axis, resulting from growth in darkness, is of especial value in the development of young plants from underground tubers, rhizomes, and seeds. When the leaves must themselves reach the light by their own elongation, as in many Monocotyledons, they act just as do the stems of Dicotyledons, and attain an abnormal length in the dark.

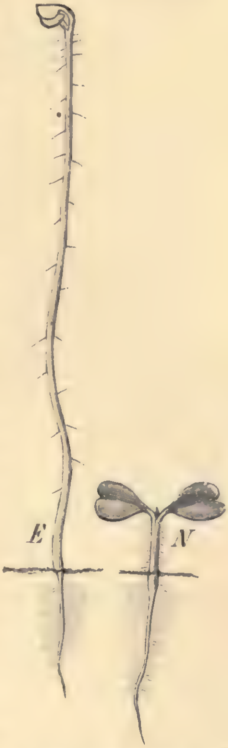


FIG. 218.—Two seedlings of *Sinapis alba*, of equal age; *E*, grown in the dark, etiolated; *N*, grown in ordinary daylight, normal. The roots bear root-hairs.

From what has already been said it would seem that plants must grow more rapidly during the night than day, and this is actually the case where other conditions affecting growth remain the same by night as by day. A too low temperature during the night may, however, completely counteract the accelerating influence of darkness upon the growth.

Just as the rays of light of different wave-length and refrangibility were found to be of different value in the process of assimilation, so growth is by no means equal in differently coloured light. IT IS TO THE STRONGLY REFRACTIVE SO-CALLED CHEMICAL RAYS THAT THE INFLUENCE OF LIGHT ON GROWTH IS DUE; the red-yellow end of the spectrum acts upon many plants in the same manner as darkness.

Radium and the Röntgen rays tend according to M. KORNICKE to arrest the processes of growth and development (^{71}).

MOISTURE exerts a twofold influence upon growth. It acts as a stimulus, and also, by diminishing transpiration, increases turgidity.

Plants in damp situations are usually larger than those grown in dry places, and in fact may differ from them in their whole habit and mode of growth. Direct contact with water seems frequently to exert a special influence upon the external form of plants. Amphibious plants, that is, such as are capable of living both upon land and in water, often assume in water an entirely different form from that which they possess in air. This variation of form is particularly manifested in the leaves, which, so long as they grow in water, are frequently linear and sessile or finely dissected, while in the air their leaf-blades are much broader and provided with petioles (cf. Fig. 35). According to M'CALLUM, *Proserpinaca palustris* forms dissected leaves even in a saturated atmosphere, while in salt solution it develops leaves with a flat lamina as in the air. The leaf-stalks and internodes also often exhibit a very different form in air and water, and undergo the same abnormal elongation as in darkness. This is especially noticeable in submerged water plants, whose organs must be brought to the surface of the water (young stems and leaf-stalk of *Trapa natans*, stem of *Hippuris*, leaf-stalk of *Nymphaea*, *Nuphar*, *Hydrocharis*). Such plants are enabled by this power of elongating their stems or leaf-stalks to adapt themselves to the depth of the water, remaining short in shallow water and becoming very long in deep water.

The great importance of free OXYGEN has already been alluded to in connection with respiration (p. 240). Without gaseous or dissolved oxygen in its immediate environment the growth of a plant entirely ceases, at least in the case of aerobionts.

MECHANICAL INFLUENCE.—Pressure and traction exert a purely mechanical influence upon growth, and also act at the same time as stimuli upon it. External pressure at first retards growth ; it then, however, acccording to PFEFFER, stimulates the protoplasm and occasions the distension of the elastic cell walls, and frequently also an increase of turgor. As a consequence of this increased turgor, the counter-resistance to the external pressure is intensified. If the resistance of the body exerting the pressure cannot be overcome, the plasticity of the cell walls renders possible a most intimate contact with it ; thus, for instance, roots and root-hairs which penetrate a narrow cavity so completely fill it that they seem to have been poured into it in a fluid state. It would be natural to suppose that the effect of such a tractive force as a pull would accelerate growth in length by aiding and sustaining turgor expansion. But the regulative control exercised by the protoplasm over the processes of growth is such that mechanical strain, as HEGLER has shown, first acts upon growth to retard it (except in the maximum of the grand periods), but then causes an acceleration of even 20 per cent. According to BALL, a constrained position may induce great thickening of the walls on particular sides (*e.g.* the convex side) of an organ.

Rarefaction of the air, chemical stimuli, and internal states may exert considerable influence on growth. In this way the formation and development of the reproductive organs, or the assumption of a twining habit may give rise to a striking elongation of the internodes together with a reduction in the size of the leaves.

According to TOWNSEND, slight wounds accelerate growth, while more serious ones retard it (72).

The Internal Development of the Organs

The internal development of the organs is only completed after they have finished their elongation and attained their ultimate size.

They are then first enabled to fully exercise their special function. To this end the cavities of certain cells usually become more or less fused, and the cell walls thickened, often in a peculiar and characteristic manner (p. 63).

Periodicity in Development and Duration of Life

The periodically recurring changes in the determinative external influences, especially in light and temperature, occasioned by the alternations of day and night and of the seasons, cause corresponding periodical variations in the growth of plants. These variations do not follow passively every change in the condition of the external influences. On the contrary, the internal vital processes of plants so accommodate themselves to a regular periodicity that they continue for a time their customary mode of growth, independently of any external change. The nightly increase of growth, which is especially noticeable after midnight in the curve of growth, and the retardation of growth, specially marked after mid-day, will continue to be exhibited for some time in prolonged darkness when the temperature remains constant. Thus under these conditions *Helianthus tuberosus* has been observed to continue its regular DAILY PERIODS for two weeks, affording an example of an after effect of the usual rhythm which suggests a comparison with the faculty of memory, and will be further considered below. According to SEMON, the usual periodicity may even be transmitted to the descendants of a plant.

Still greater is the influence exerted on the life of plants by the alternation of winter and summer, which in the plants of the colder zones has rendered necessary a well-marked winter rest. This is not in reality an absolute rest; for although the outwardly visible processes of development and growth stand still, the internal vital processes, although retarded, never altogether cease.

The ANNUAL PERIODS of growth occasioned by climatic changes, which are rendered so noticeable by the falling of the leaves in the autumn, and the development of new shoots and leaves in the spring, have stamped themselves so indelibly upon the life of the trees and shrubs of the temperate zones, that, when cultivated in tropical lands where other plants are green and blossom and bear fruit throughout the year, they continue to lose their leaves and pass for a short time at least into a stage of rest. The Oak, Beech, Apple, and Pear retain their resting period in the sub-tropical climate of Madeira, while, under uniformly favourable conditions in the mountain regions of Java, the periodicity may be disturbed in particular individuals. This even occurs in the several branches of the same tree which may then bear leafy and leafless boughs at the same time (Oaks, Magnolias, Fruit and Almond trees, together with some endemic species). Other trees again gradually accustom themselves to the new conditions, as the Peach, for instance, which in Ceylon has become an evergreen tree. The Peach is reported to produce flowers and fruit throughout the entire year; while the Cherry, like many other trees of the temperate zone, ceases altogether to bear flowers in tropical climates.

Since in these tropical localities endemic species may exhibit well-marked periods of rest and of renewed vegetative activity, it is clear that such periodicity is not merely induced and regulated by external influences. Its cause must rather be sought in an autonomous, rhythmic course of the vital process itself. Although to so many plants winter is the season of rest and cessation from growth, other plants, *e.g.* certain Lichens and Mosses, seem to find in the warmer days of winter the most favourable conditions of vegetation ; and in summer, on the contrary, either do not grow at all or only very little. Similarly, many spring plants attain their highest development, not in summer, but during the variable weather of March and April, and, for the most part, they have entered upon their period of rest when the summer vegetation is just awakening.

In countries where there are alternate rainy and dry periods, the latter generally corresponds to the period of vegetative rest.

Favourable conditions may shorten the resting period, especially if the organisms have previously been exposed to the influence of frost, drought (withering), or, as JOHANNSEN discovered, to ether vapour, etc. This premature awakening does not, however, result equally readily at all periods of the resting time. It occurs best in the later portion of the latter, just before the normal time of awakening, and almost equally well in the earlier portion just after arrest has taken place. Potato tubers and bulbs in some cases do not completely enter into a resting state before their development is awakened. In the intervening period of complete rest such attempts are usually without result. These facts must be considered in the forcing of plants, as must also the fact of the temperature optima differing for the several developmental processes, for some of which they are relatively low (73).

DURATION OF PLANT LIFE.—The life of a plant, during the whole of its development, from its germination to its death, is dependent upon external and internal conditions. In the case of the lower vegetable organisms, such as Algae, Fungi, and Bacteria, their whole existence may be completed within a few days or even hours, and indeed some of the higher herbaceous plants last only for a few weeks, while the persistent shrubs and trees, on the other hand, may live for thousands of years.

After the formation of the seeds, there occurs in many plants a cessation of their developmental processes, and such a complete exhaustion of vitality that death ensues. Such an organic termination of the period of life occurs in our annual summer plants, which, according to KLEBS, can be made perennial by artificially preventing their reproduction. It also takes place with plants in which the preparatory processes for the formation of fruit have extended for two or more years, as in biennial plants in the case of the 10- to 40-year-old Agave, which, after the formation of its stately inflorescence, dies of exhaustion, and in some Palms (*Corypha umbraculifera*). In plants, on the other hand, which in addition to the production of flowers and fruit accumulate also a reserve of organic substance, and, with their reproductive organs, form also new growing points, life does not cease with the production of the seeds. Such plants possess within themselves the power of unlimited life, the duration of which may only be terminated by unfavourable external conditions, the ravages of parasites, injuries from wind, and other causes.

The longevity of trees having an historical interest is naturally best known and most celebrated, although, no doubt, the age of many other trees, still living, dates back far beyond historical times. The celebrated Lime of Neustadt in Wurtemberg is nearly 700 years old. Another Lime 25·7 m. in circumference had 815 annual rings, and the age of a Yew in Braburn (Kent) which is 18 m. in circumference is estimated at 2880 years. A stem of a *Sequoia* in the Berlin Museum has, with 1360 annual rings, a diameter of 4·7 m., from which an idea can be formed of the age of those trees which have attained a diameter of 16 m. An *Adansonia* at Cape Verde, whose stem is 8-9 m. in diameter, and a Water Cypress (*Taxodium mexicanum*) near Oaxaca, Mexico, are also well-known examples of old trees. Of an equally astonishing age must have been the celebrated Dragon tree of Orotava, which was overturned in a storm in 1868, and afterwards destroyed by fire. The lower plants also may attain a great age; the apically growing mosses of the calcified *Gymnostomum* clumps, and the stems of the Sphagnaceae, metre-deep in a peat-bog, must certainly continue to live for many centuries (74).

In thus referring to the ages of these giant plants, it must not be understood that all the cells remain living for so long a time, but rather that new organs and tissues are developed, which continue the life of the whole organism. All that is actually visible of a thousand-year-old Oak is at most but a few years old. The older parts are dead, and are either concealed within the tree, as the pith and wood, or have been discarded like the primary cortex. The cells of the original growing point have alone remained the whole time alive. They continue their growth and cell division so long as the tree exists; while the somatic cells of the permanent tissue arising from them, and destined for particular purposes, all lose their vitality after a longer or shorter performance of their functions.

The cells of the root-hairs often live for only a few days; the same is also true of the glandular cells and trichomes of stems and leaves. The wood and bast fibres, as also the sclerenchymatous cells, lose their living protoplasm after a short time. Entire organs of long-lived plants have frequently but a short existence; the sepals, petals, and stamens, for example. The foliage leaves, also, of deciduous trees live only a few summer months and then are discarded. The leaves even of evergreen plants continue living but a few years, before they too fall off. Small twigs, especially of Conifers, are also subject to the same fate. The cells of the medullary rays afford the best examples of long-lived cells constituting permanent tissues. In many trees, as in the Beech, living medullary ray cells over a hundred years old have been found, although, for the most part, they live only about fifty years.

V. The Phenomena of Movement

In every living organism there is constantly occurring in the course of the metabolic processes an active movement and transposition of substance. As these movements are for the most part molecular they are generally imperceptible; but that they actually take place is demonstrated with absolute certainty by the local accumulation and diminution of substance.

There are also other forms of movement which play an important part in the physiology of every organism, and on which its vital processes are to a large extent dependent: these are the movements due to heat and the related conditions of vibration resulting from light, electricity, etc.

Apart from the movements of this class, which may take place within organisms which, externally, are apparently at rest, there occur also in plants actual CHANGES IN POSITION, externally noticeable but usually of gradual operation; in special cases they may involve rapid motion. These movements may be carried on either by the whole plant or by single organs.

Reference is here made only to the SPONTANEOUS MOVEMENT resulting from the activity of a plant organism itself, and this should not be confused with the PASSIVE movements due to externally operating mechanical agencies, such as water and wind, which, although they have a certain importance for plant life, will not be here considered.

PROTOPLASM itself is capable of different movements. Naked protoplasmic bodies almost always show slow movements resulting in a gradual change of position; but cells enclosed by cell walls possess also the power of INDEPENDENT LOCOMOTION, often indeed to a considerable extent. Multicellular plants, however, as a rule ultimately attach themselves, by means of roots or other organs, to the place of germination, and so lose for ever their power of locomotion, except in so far as it results from growth. A gradual change in position due to growth is apparent in plants provided with rhizomes, the apical extremities of which are continually growing forward, while the older portions gradually die off. A yearly elongation of 5 cm. in the apical growth of the rhizomes would result, in twenty years, in moving the plant a distance of one metre from its original position. A seedling of *Cuscuta* in its search for a host plant illustrates the power of maintaining, for a time, a creeping movement over the surface of the soil; a growing *Caulerpa* (Fig. 295) likewise exhibits in the course of years a similar advancing movement. In addition to these movements, occasioned by a growth in length, plants firmly established in the soil possess also the power of changing the position and direction of their organs by means of CURVATURE and ROTATION. In this way the organs are brought into positions necessary or advantageous for the performance of their function. By this means, for example, the stems are directed upwards, the roots downwards; the upper sides of the leaves turned towards the light, climbing plants and tendrils twined about a support, and the stems of seedlings so bent that they break through the soil without injury to the young leaves.

Movements of Naked Protoplasts and Single Cells

The creeping movements of naked protoplasts, such as are shown by an amœba or plasmodium, in the protrusion, from one or more sides, of protuberances which ultimately draw after them the whole protoplasmic body, or are themselves again drawn in (Fig. 219), are distinguished as AMŒBOID MOVEMENTS. These movements resemble, externally, the motion of a drop of some viscid fluid on a surface to which it does not adhere, and are chiefly due to surface tension, which the protoplasm can at different points increase or diminish, by means of its quality of irritability. By means of irregular changes of surface-tension similar amœboid movements are also exhibited by drops of lifeless fluids, such as drops of oil in soap solution; or drops of mercury in 20 per cent solution of potassium nitrate in contact with crystals of potassium bichromate.

In the SWIMMING MOVEMENTS BY MEANS OF CILIA, on the contrary, the whole protoplasmic body is not involved, but it possesses special organs of motion in the form of whip-like FLAGELLA or CILIA. These may be one, two, four, or more in number, and arranged in various ways (Figs. 97, 98). They move very rapidly in the water and impart considerable velocity to the protoplast, often giving it at the same time a rotary movement. The minute swarm-spores of *Fuligo varians* traverse 1 mm. (sixty times their own length) in a second, those of *Ulva*, 0·15 mm., while others move more slowly. The *Vibrio* of Cholera, one of the most rapidly moving bacilli, takes 22 seconds to traverse a millimetre. The ciliary movement is so regulated as to propel the protoplast in a definite direction.

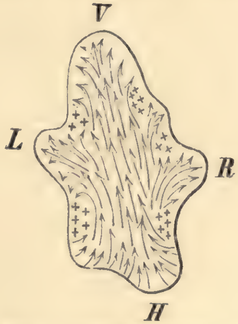


FIG. 219.—Amœboid movement. The arrows indicate the direction and energy of the movement; the crosses, the points at rest. At the time being the principal movement is from *H* to *V*, but at any moment it may be towards *R* or *L*, and so change the direction of the course taken by the amœba.

Gravity and light, certain substances in solution, and mechanical hindrances are the principal influences which regulate the movements of free-swimming protoplasmic bodies and cells. The direction of the movements of the swarm-spores of Algae are chiefly determined by the light. So long as they remain in darkness they move through the water in all directions; but as soon as they are illuminated from one side only, a definite direction in their movements is perceptible. They move either straight towards the light or turn directly away from its source. Their retrogressive movements from the light occur either in case of too intense illumination, or at a certain age, or through some unknown disturbing irritation. The advantage of such HELIOTACTIC MOVEMENTS (phototactic) is at once apparent when the part taken by the swarm-spore in the life of an Alga is considered. In order to provide for the future nutrition of the stationary Alga into which it afterwards develops, it must seek the light. If a point with suitable (that is, not too intense and not too weak) illumination be attained, then the swarm-spore must attach itself by the end which carries the cilia : to do this it must turn itself from the light towards a dark object. On the other hand, as the swarm-spores do not come to rest at all in absolute darkness, but swim continuously until thoroughly exhausted, the possibility of their attaching themselves in a spot devoid of light where the new plant could not assimilate is excluded.

The swarm-spores of aquatic Fungi and spermatozoids, according to PFEFFER'S investigations, are chiefly influenced in their movements by the unequal distribution of dissolved substances in their environment (topotaxis). The crowding together of Bacteria appears, from ROTHERT'S experiments, not to be due to movement towards an attracting stimulus but to their inability to leave a point of optimal concentration reached by accident ; the decline in this concentration arrests their movement and prevents their dispersal (phobotaxis). Minute traces of free oxygen can be recognised by the influence exerted on the movement of certain Bacteria ; ENGELMANN'S bacterial method of demonstrating assimilation depends on this fact. According to their momentary requirements and their sensitiveness to stimuli, such small organisms move either towards or away from the points of highest concentration ; they are sensitive to the quantity as well as the quality of the dissolved substances, and also to the osmotic effects of the latter (osmotaxis) (75).

As the result of similar CHEMOTACTIC MOVEMENTS spermatozoids approach the female sexual organs. PFEFFER has demonstrated that the spermatozoids of Ferns are enticed into the long necks of the archegonia by means of malic acid : while the archegonia of the Mosses attract the spermatozoids by a solution of cane-sugar, and those of the Marchantiaceae by proteid substances. In such cases an extremely small quantity of dissolved substance is often a sufficient stimulus to call forth active chemotactic movements ; a 0·001 per cent solution of malic acid suffices for the attraction of Fern spermatozoids. The movements of amœbæ and plasmodia are similarly induced by external influences. These naked protoplasts live not only in water but also in moist substrata (plasmodia, amœbæ), and seem to possess the power of seeking out situations with more moisture, or of avoiding them (before the formation of spores) : their movements are also influenced by the direction of currents in the water (rheotaxis). The term thigmotaxis or stereotaxis has been applied to the exceptional property of certain swarming cells, which are stimulated by mechanical contact to remain attached to the object around which they are swarming. This has been observed in spermatozoids of Fucaceae and in *Chromatium weissii*, a sulphur Bacterium. The fact that algal swarm-spores on a hard rough substratum form stronger attaching organs than on a smooth surface is related in some degree to this. In cases where cells enclosed by cell walls (*e.g. Haematococcus pluvialis*) swim freely about by means of cilia, the cilia spring from the protoplasm and pierce the cell walls.

Diatoms and Desmids exhibit quite a different class of movements. The Diatoms glide along, usually in a line with their longitudinal axes, and change the direction of their movements by oscillatory motions. From the manner in which small particles in their neighbourhood are set in motion, it was concluded that special organs of motion probably protrude, like pseudopodia, through openings in their hard silicified shell. Recently these motile organs have been seen in some forms. According to O. MÜLLER, the movement is set up by a current of protoplasm, which bursts through the raphe ; this may become invested with a mucilaginous sheath. Corresponding to the differences in the construction of the membrane, differences in the motile apparatus are found in the group. The cells of Desmidiaceae attach themselves to the substratum by mucilaginous excretions, and effect their peculiar movements by local fluctuations in the mucilaginous layer. The advancing movements of the filamentous Oscillarieae and Spirulinae take place, according to CORRENS, in a mucilaginous sheath, but their mechanism is as little understood as that of the slow movements of *Spirogyra*.

The Movements of Protoplasm within Walled Cells

Although plants which are firmly attached and stationary exhibit no such locomotory movements, the protoplasm within their cells does possess a power of movement. Such internal protoplasmic movements are especially active in the non-cellular Siphoneae, and in non-septate Fungi in the elongated internodal cells of the Characeae, in the hairs of many plants, as well as in the leaf-cells of some aquatic plants.

The three following different forms of protoplasmic movement within cell cavities may be distinguished : CIRCULATION, ROTATION, and ORIENTATION.

In the case of CIRCULATORY MOVEMENT the different currents of protoplasm, although often quite close together, flow in different directions in slender protoplasmic strands, which stretch from the cell wall to the nucleus (cf. p. 58 and Fig. 60).

In the ROTATORY MOVEMENT the protoplasm moves along the cell wall in one direction only, dragging with it the nucleus and often also the chlorophyll grains (cf. p. 58).

The cause of these movements, which may take different directions in adjoining cells, and may also continue after the protoplasm has been drawn away from the cell walls by plasmolysis (p. 180), is not yet understood. It is, however, known that the continuance and activity of such protoplasmic movements, the existence of which was first observed by CORTI in 1772, and later rediscovered by TREVIRANUS in 1807, are dependent on factors which, in general, support and promote the vital activity ; while the presence of free oxygen and proper conditions of temperature seem to be particularly favourable to them. That the movements in *Nitella* continued, according to KÜHNE's observations, for days and weeks in the absence of oxygen is explained, according to RITTER, by the power the Characeae possess of becoming facultative anaerobes. Those Bacteria which are obligate anaerobes lose their power of motion in the presence of oxygen. From the study of sections in the cells of which currents had been induced in the protoplasm, by the injuries sustained in their preparation and by other abnormal conditions, grave errors have arisen concerning the existence of such protoplasmic movements in cells, in which under normal conditions they cannot be observed. The presence of protoplasmic currents in a cell may, in fact, indicate either an energetic vital activity, or, on the other hand, be merely a symptom of a pathological or, at least, of an excited condition of the protoplasm (^{76}).

The movements of orientation of the protoplasmic body are usually so gradual as to be only recognisable through their operations. They are induced by changes in the external influences, especially as regards the intensity of the light, and result in producing a definite position of the protoplasmic bodies, as, for example, the orientation of the chlorophyll grains with regard to the light. Movements of this kind have been most frequently observed in Algae, in submerged Duckweed (*Lemna trisulca*), in the prothallia of Ferns and Mosses; but similar movements can also be observed in the higher plants.

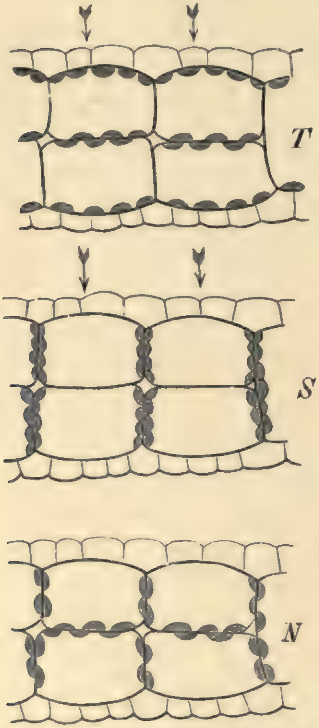


FIG. 220.—Varying positions taken by the chlorophyll grains in the cells of *Lemna trisculca* in illumination of different intensity. *T*, in diffuse daylight; *S*, in direct sunlight; *N*, at night. The arrows indicate the direction of the light. (After STAHL.)

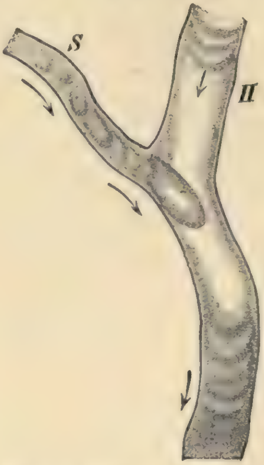


FIG. 221.—Streaming protoplasm in the hyphæ of *Rhizopus nigricans*. (After J. C. ARTHUR.)

In the cells of the filamentous Alga *Mesocarpus*, the chloroplasts, in the form of a single plate suspended length-wise in each cell, turn upon their longitudinal axes according to the direction and intensity of the light. In light of moderate intensity, according to STAHL's observations, they place themselves transversely to the source of light, so that they are fully illuminated (transverse position); when, on the other hand, they are exposed to direct sunlight, the chlorophyll plates are so turned that their edges are directed towards the source of light (profile position). A similar protection of the chloroplasts against too intense light, and their direct exposure, on the other hand, to moderate illumination, is accomplished, where they are of a different form and more numerous, by their different disposition relatively to the cell walls. In moderate light the chlorophyll bodies are crowded along the walls, which are at right angles to the direction of the rays of light (Fig. 220 *T*). They quickly pass over to the walls parallel to the rays of light, however, as soon as the light becomes too intense, and so retreat as far as possible from its action (Fig. 220 *S*). In darkness or in weak light the chloroplasts group themselves in still a third way (Fig. 220 *N*), the advantage of which is not altogether clear. Similar changes of position may result from certain substances in solution in the surrounding water.

The form of the chlorophyll bodies themselves undergoes modification during changes in their illumination; in moderate light they become flattened, while in light of greater intensity they are smaller and thicker.

As a special mode of protection against too intense light, the chloroplasts of the Siphoneae and Diatomeae (and the same thing is observed in many plants) become balled together in separate clumps. In correspondence with the changes in the position of the chloroplasts, the colouring of green organs naturally becomes modified. In direct sunshine they appear lighter, in diffused light a darker green. The attention of SACHS was first called to the phenomena of the movements of the chloroplasts by the accidental observation that the shadow of a thermometer was represented in dark green on a leaf otherwise directly illuminated by the sun.

Wounds and cell-wall thickenings localised to one side of the cell likewise give rise to orientation movements, as they occasion a crowding together on one side of the nucleus and protoplasm.

A peculiar mode of protoplasmic movement, which may be termed STREAMING, occurs, according to ARTHUR, in the non-septate mycelium of some Fungi. In it the whole mass of protoplasm, with its included vacuoles, streams towards the end of the hypha, only the limiting layer remaining at rest. After a longer or shorter interval a similar streaming movement sets in in the opposite direction (cf. Fig. 221).

TERNETZ observed the same type of movement in the mycelium of *Ascophanus carneus*, where the protoplasmic stream, with its vacuoles, makes its way through the pores of the perforated transverse septa. In this latter case it was established that the direction of streaming was determined by local differences in the supply of water (77).

Movements producing Curvature

The movements of the organs of stationary plants, unicellular as well as multicellular, are accomplished by means of curvatures. In an organ that has grown in a straight line the longitudinal sides are all of equal length; in an organ that is curved, however, the concave side is necessarily shorter than the convex side. When, accordingly, the opposite sides of a pliable organ become of unequal length, the organ must curve toward the shorter side (Fig. 175). Inequality in the length of the opposite sides may result from various causes. A curvature occurs if the length of one side remains constant, while the opposite side becomes shorter or longer, and also from the unequal elongation or contraction of both sides, or from the elongation of one side and the contraction of the other.

Such curvatures most frequently occur in plants as a consequence of UNEQUAL GROWTH. More rarely they are due to the different length of the opposite sides, resulting from unequal TURGOR TENSION. A third source of curvature is found in the unequal amount of water taken up by IMBIBITION, and the consequent unequal swelling of the cell walls on the opposite sides of an organ. A fourth cause is the loss of water from certain cell-complexes, the latter being made to contract in a definite direction owing to the cohesive force of the water which remains in them.

When the direction of the curvature is determined by the position of the source of the stimulus causing it, the movement is termed tropic (tropism); when no such relation is evident and the movement results from the internal disposition of the structure, it is spoken of as nastic.

1. Movements dependent on Imbibition and Cohesion

As the cell walls of actively living cells are always completely saturated with imbibition water, hygroscopic curvatures are exhibited only by dry or drying and, for the most part, dead tissues. The hygroscopic movements in any case, however, are due to the physical properties of the cell walls, and have no direct connection with the vital processes, except in so far as the capacity of cell walls to swell and take up large quantities of imbibition water is due to the protoplasm by which they were formed. The activity of the protoplasm in the formation of the cell walls is likewise manifested in their anatomical structure, in their stratification and striation, and in the position of the pits.

The absorption of imbibition water by cell walls is accompanied by an increase in their volume, and conversely the volume of the cell walls is diminished by the evaporation of the imbibition water. Accordingly, whenever unequal amounts of water are held by the cell walls on the different sides of an organ, either through unequal absorption or evaporation, hygroscopic movements are produced, which result in the curvature of the organs. In many cases the organs of plants are especially adapted to such movements, by means of which, in fact, important operations are often accomplished, as, for example, the dehiscence of seed-vessels and the dissemination and burial of seeds. Similar movements also occur, without special purpose, however, as for example in dead branches of Conifers.

The rupture of ripe seed-vessels, as well as their dehiscence by the opening of special apertures (*Papaver*, *Lychnis*, *Antirrhinum*, etc.), is a consequence of the unequal contraction of the cell walls due to desiccation. At the same time, through the sudden relaxation of the tension, the seeds are often shot out to a great distance (Tricoccae, *Geranium*, etc.). In certain fruits not only curvatures but torsions are produced as the result of changes in the amount of water they contain, *e.g.* *Erodium gruinum* (Fig. 222), *Stipa pennata*, *Avena sterilis*; by means of these, in conjunction with their stiff barb-like hairs, the seeds bury themselves in the earth.

The variation in dampness of the air causes the pappus hairs of the Cynareae (Compositae) to expand in dry and fold together in damp weather. The opening or closing of the moss sporogonium is, in like manner, due to the hygroscopic movements of the teeth of the peristome surrounding the mouth of the capsule. In the case of the Equisetaceae the outer walls of the spores themselves (the perinium) take the form of four arms, which, like elaters, are capable of active movements, by means of which numbers of spores become massed together before germinating, and the isolation of the diœcious prothallia prevented (Fig. 420 E).

In order to call forth imbibition movements the actual presence of liquid water is not necessary; for the cell walls have the power of absorbing moisture from the air. They are hygroscopic, and for this reason the ensuing movements are also often termed hygroscopic movements.

STEINBRINCK and KAMERLING have distinguished the mechanisms which depend on the cohesive power of water from those depending on imbibition. The cohesion mechanisms were previously confounded with the latter, from which they differ in that, even during the movement, the cell walls remain saturated with water. It is the lumen of the cell which diminishes in size when the loss of water, on which the movement depends, occurs. The cohesive force of the diminishing amount of water tends to pull the thinner walls of the cell inwards after it, and thus to approximate other walls, which are strongly thickened and exhibit a definite arrangement. In this way an energetic shortening of the specialised tissue is brought about which leads to alteration of form or to the dehiscence of spaces enclosed by the tissue. The walls of anthers and of the sporangia of the higher cryptogams afford examples of such a method of dehiscence. The movements of the elaters of Liverworts and Myxomycetes, which serve to distribute the spores, as well as of the pappus of most, and the involucre of some, Compositae, are effected in the same way (78).

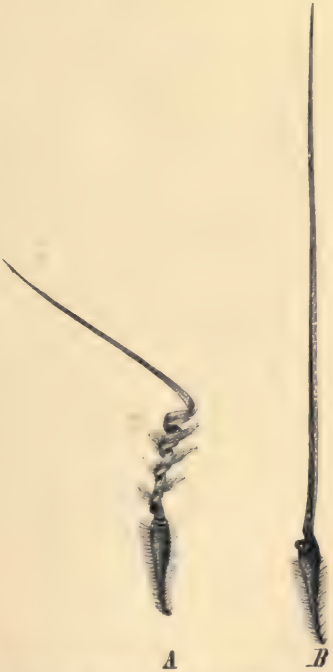


FIG. 222.—Partial fruit of *Erodium gruinum*. *A*, in the dry condition, coiled; *B*, moist and elongated.

Mechanisms dependent on imbibition and on cohesion may cooperate in the movements of some plants.

2. Growth Curvatures

Movements from which curvatures result are, for the most part, produced by the unequal growth of living organs. The unequal growth is due, partly to internal causes which are still undetermined, and partly to the operation of external influences. The movements resulting in the first case are spontaneous, and are called AUTONOMIC MOVEMENTS or NUTATIONS; in the second case the movements are the result of external stimuli, and are distinguished as IRRITABLE or PARATONIC (AITIONOMIC) MOVEMENTS.

Autonomic Growth Curvatures (Nutations) are most plainly apparent in young actively-growing organs, although nutations have been shown to be exhibited by all growing plants, as their tips do not grow forward in a straight line, but, instead, describe irregular elliptical curves. These movements, which Darwin termed CIRCUMNUTATIONS, while often not perceptible to the eye, are very noticeable is some special organs.

The unfolding of most leaf and flower buds, for example, is a nutation movement which, in this instance, is induced by the more vigorous growth of the inner side of the young leaves. The same unequal growth manifests itself most noticeably in the leaves of Ferns and many Cycadeae. In the same manner, movements of nutation are caused in lateral axes when growth is more energetic on either the upper side (EPINASTY) or on the lower side (HYPONASTY). Epinastic curvatures are often greatly increased when poisonous gases are present in the air, and may also be started by the organ's own weight. This is termed "load-curvature" by WIESNER. The stems of many seedlings are, on their emergence from the seeds, strongly curved. By the nutation of the shoots of *Ampelopsis quinquefolia* a curvature is produced which continuously advances with the increased growth; so that, by means of its hooked extremity, a shoot is better enabled to seek out and cling to a support. When the unequal growth is not confined to one side, but occurs alternately on different sides of an organ, the nutations which result seem even more remarkable. Such movements are particularly apparent in the flower-stalk of an Onion or of *Yucca filamentosa*, which, although finally erect, in a half-grown state often curves over so that its tip touches the ground. This extreme curvature is not, however, of long duration, and the flower-stalk soon becomes erect again and bends in another direction. Thin and greatly elongated organs (*e.g.* tendrils) must, from purely physical reasons, quickly respond to the effects of unequal growth. If the line of greatest growth advances in a definite direction around the stem, its apex will exhibit similar rotatory movements (REVOLVING NUTATION). This form of nutation is characteristic of the tendrils and shoots of climbing plants, and facilitates their coming in contact with a support. The so-called REVOLVING NUTATION OF TWINING PLANTS is not, however, an AUTONOMIC MOVEMENT, and will be considered later with the paratonic movements.

Paratonic (Aitionomic) Growth Curvatures.—The paratonic movements are of the very greatest importance to plant life, for through their operations the organs of plants first assume such positions in air, or water, or in the earth as are necessary for the performance of their vital functions. A green plant which spread its roots over the surface and unfolded its leaves below ground could not exist, even though all its members possessed the best anatomical structure. Seeds are not always deposited in the soil with the embryonal stem directed upwards and the radicle downwards, so that their different organs can, merely by direct growth, attain at once their proper position. A gardener does not take the trouble to ascertain, in sowing seed, if the end which produces the root is directed downwards or the stem end upwards; he knows that in any position the roots grow into the ground and the stems push themselves above the surface. Plants must accordingly have in themselves the power of placing their organs in the positions best adapted to the conditions of their environment. That is only possible, however, when the externally operative forces and substances can so influence the growth of a plant that it is constrained to take certain definite directions.

The same external influences excite different organs to assume quite different positions. Through the influence of gravity, the tap-root grows directly downwards in the soil, while the lateral roots take a more or less oblique direction. The main stem grows perpendicularly upwards; it, like the primary root, is ORTHOTROPIC. The lateral branches, on the other hand, just as the secondary roots, assume an inclined position and are PLAGIOTROPIC. The apical extremities of shoots are constrained to seek the source of light; the leaves, on the contrary, under the same influence place their surfaces transversely to the direction of the rays of light. The property whereby an organ, when acted upon by external influences, assumes different positions has been termed ANISOTROPY by SACHS. In addition to the purely morphological structure of the plant body, anisotropy also determines essentially its external form and appearance, or what is termed the habit of the plant (79).

That all these paratonic movements cannot result merely from the physical action of external forces will be at once recognised if it be taken into consideration that anisotropic but in other respects similar organs are affected differently by the same influences, and that even the same organs react differently at different ages; moreover, the external forces produce effects which bear no relation to their usual physical and chemical operations. It will, on the contrary, be at once apparent that the movements are rather the result of definite processes of growth, arising from an irritability to stimuli induced by external influences (cf. pp. 4, 174).

In order that external influences may produce such effects, plants must be sensitive to stimuli, that is, the stimuli must produce in them certain modifications with which, in turn, certain definite vital actions are connected. The precise manner in which an external influence produces an internal reaction within an organism is not at present known. In order that an external physical force can operate as a stimulus, there must exist within the living substance definite structures or organs which are influenced by it. Thus, for example, HABERLANDT and NEMEC regard the pressure of starch grains (the position of which in the cell is determined by their weight) on the more or less receptive parts of the limiting layer of the protoplast as the arrangement for perceiving the direction of gravity (statolith theory). The movements of growth occasioned by external stimuli are, for the most part, movements in response to directive stimuli which lead to a definite position of the organ, relatively to the direction of the operative influence. The principal external stimuli that come into consideration are light, heat, gravity, chemical influences (oxygen, nutritive substances, water, etc.), impact and friction.

As the points of greatest irritability in plants or their organs are often more or less removed from the points where the effect of the stimulation is manifested, a propagation of the stimulation must take place. Thus directive stimuli are received by the apices of organs which do not themselves carry out the movement, but transmit it to the regions in which the movement takes place. In roots the geotropic stimulus is mainly perceived by the root tip; in grass-seedlings the stimulus of light is perceived by the tip of the cotyledonary sheath; in the tentacles of *Drosera* the contact stimulus affects the glandular swelling at the tip and induces the movement in the portions nearer the base. According to MIEHE even when the growing points are not the only perceptive regions they exercise a controlling influence over the resulting movements of curvature (80).

The capacity of organs to assume a definite direction by means of curvatures of growth is distinguished, according to the nature of the particular exciting stimulus, as heliotropism, geotropism, hydrotropism, etc.; and these again are either POSITIVE or NEGATIVE, according as the direction taken by the curvature is towards or away from the source of the stimulus. Plant organs which place themselves more or less transversely to the line of action of the operative forces are termed DIATROPIC. As a special result of diatropism, a transverse position is assumed which is exactly at right angles to the direction in which the influence which acts as the stimulus is exerted. Dorsiventral organs, in particular, exhibit a tendency to assume diatropic or transverse positions.

A. *Heliotropism*

The importance of light to plant life is almost incalculable. It is not only absolutely essential for the nutrition of green plants, but it has also a powerful effect upon the growth and general health of the plant. Deprived of light for any length of time, leaves and flowers usually fall off; fully developed, vigorous organs of green plants soon become yellow in the dark, and droop and die. Prolonged darkness acts like a poison upon those portions of plants accustomed to the light. On the other hand, exactly the reverse is true of plants or organs whose normal development is accomplished in darkness.

Upon them the light has a most injurious, even fatal, effect, as may be easily observed in the case of Fungi and Bacteria. The hygienic importance of daylight in dwelling-places is due to the destructive action of light upon such forms of plant life. That some plants seek the light, while others avoid it, is not surprising in view of the adaptability which organisms usually exhibit in respect to the influences with which they come in contact in the natural course of their development.

A good opportunity for the observation of heliotropic phenomena is afforded by ordinary window-plants. The stems of such plants do not grow erect as in the open air, but are inclined towards the window, and the leaves are all turned towards the light as if seeking help. The leaf-stalks and stems are accordingly POSITIVELY HELIOTROPIC. In contrast with these organs the leaf-blades take up a position at right angles to the rays of light in order to receive as much light as possible. They are diaheliotropic, or TRANSVERSELY HELIOTROPIC, in the strictest sense (Fig. 223). If among the plants there should be one with aerial roots, *Chlorophytum* for instance, an example of NEGATIVE HELIOTROPISM will be afforded, as the aerial roots will be found to grow away from the window and turn towards the room.

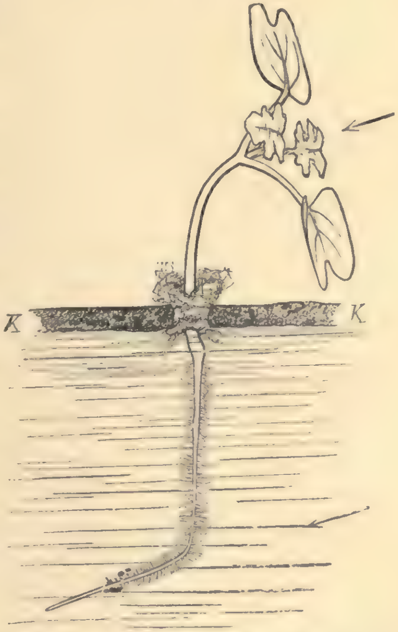


FIG. 223.—A seedling of the White Mustard in a water culture which has first been illuminated from all sides and then from one side only. The stem is turned towards the light, the root away from it, while the leaf-blades are expanded at right angles to the incident light. *K K*, Sheet of cork to which the seedling is attached.

For more exact investigation of heliotropic movements it is necessary to be able to control more accurately the source and direction of the light. This can be best accomplished by placing the plants in a room or box, lighted from only one side by means of a narrow opening or by an artificial light. It then becomes apparent that the direction of the incident rays of light determines the heliotropic position; every alteration in the direction of the rays produces a change in the position of the heliotropic organs. The apical ends of positively heliotropic organs will be found to take up the same direction as that of the rays of light.

The exactness with which this is done is illustrated by an experiment made with *Pilobolus crystallinus* (Fig. 224). The sporangiophores of this Fungus are quickly produced on moist horse or cow dung. They are positively heliotropic, and turn their black sporangia towards the source of light. When ripe these sporangia are shot away from the plant, and will be found thickly clustered about the centre of the glass covering a small aperture through which alone the light has been admitted; a proof that the sporangiophores were all previously pointed exactly in that direction (81).

Upon closer investigation of the manner in which the POSITIVE HELIOTROPIC CURVATURE of an organ is accomplished, it is found THAT THE SIDE TURNED TOWARDS THE LIGHT GROWS MORE SLOWLY, THE SIDE AWAY FROM THE LIGHT MORE RAPIDLY THAN WHEN ILLUMINATED FROM ALL SIDES. This may be readily shown by previously marking with Indian ink regular intervals from one to two millimetres apart on the opposite sides of the organ. After the curvature has taken place the intervals between the marks will be found to be much farther apart on the shaded side than on the side turned to the light. As compared with the elongation under normal conditions of growth, the marks on the illuminated side have remained nearer together, while those on the shaded side have drawn farther apart; that is, the growth in the case of a positive heliotropic curvature has been retarded on the illuminated side and promoted on the shaded side. It also becomes evident, from observation of the ink-marks, THAT CURVATURE TAKES PLACE ONLY IN THE PORTIONS OF STEMS STILL IN PROCESS OF GROWTH, AND THAT THE CURVATURE IS AS A RULE GREATEST WHERE THE GROWTH IS MOST VIGOROUS.

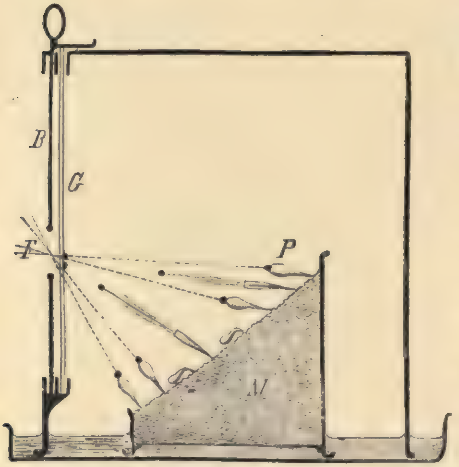


FIG. 224.—*Pilobolus crystallinus* (*P*), abjecting its sporangia towards the light. *G*, Sheet of glass; *B*, opaque case with a circular opening at *F*; *M*, vessel containing horse-dung. (Cf. description in text.)

It was formerly believed that the increased growth of the shaded side was produced by the beginning of etiolation, and that the diminished growth on the illuminated side was due to the retarding effect which light exerts upon growth in length (p. 258). Other heliotropic phenomena were found to be at variance with this explanation of heliotropism. Unicellular perfectly transparent fungal hyphæ are also subject to positive heliotropic curvature, although in this instance there can be no shaded side; on the contrary, the side of a hypha turned away from the light is especially illuminated on account of the refraction of the light rays. The fact, too, that negative heliotropic curvatures also take place renders it evident that heliotropism cannot be due to one-sided etiolation; for in negative heliotropism the side most directly illuminated is the one that grows more rapidly, although the retarding effect of light on the normal growth in length of negatively heliotropic organs is equally operative (roots, rhizomorpha).

It is evident from these considerations that it is not the difference in the intensity of the light which causes the heliotropic curvatures, but the direction in which the most intense light rays enter the organs. LIGHT ACTS AS A MOTORY STIMULUS WHEN IT PENETRATES AN ORGAN IN ANY OTHER DIRECTION THAN THAT WHICH CORRESPONDS WITH THE POSITION OF HELIOTROPIC EQUILIBRIUM.

The heliotropic curvatures are most strongly produced, just as in the case of the heliotactic movements of freely moving swarm-spores, by the blue and violet rays, while red and yellow light exerts only an extremely slight influence, or none at all. It is due to the fact that the red-yellow and blue-violet rays are always present together in daylight, that the heliotropism of the leaves is of advantage to their assimilatory activity. Intermittent illumination has a more powerful effect on the plant than light of uniform intensity.

Sensibility to heliotropic influences is prevalent throughout the vegetable kingdom. Even organs like the roots of trees, which are never under ordinary circumstances exposed to the light, often exhibit heliotropic irritability. Positive heliotropism is the rule with aerial vegetative axes. Negative heliotropism is much less frequent; it is observed in aerial roots, and sometimes also in climbing roots (Ivy, *Ficus stipulata*, *Begonia scandens*), in the hypocotyl of germinating Mistletoe, in many, but not all, earth roots (*Sinapis*, *Helianthus*), in tendrils (chiefly in those with attaching discs), and in the stems of some climbers. By means of their negative heliotropic character, the organs for climbing and attachment turn from the light towards, and are pressed firmly against, their support.

Negative heliotropic curvatures are occasionally produced, not in the region of most rapid growth, but in the older and more slowly growing portions of the stem. The stems of *Tropaeolum majus*, for example, exhibit positive heliotropic curvatures in the region of their greatest elongation, but lower down the stems, where their growth is less rapid, become negatively heliotropic.

TRANSVERSE HELIOTROPISM is confined almost solely to leaves and leaf-like assimilatory organs, such as Fern prothallia and the thalli of Liverworts and Algae. In these organs transverse heliotropism, in conformity with its great utility for assimilation, predominates over all other motory stimuli. Thus it is possible to cause the leaf-blades of a *Malva* or a *Tropaeolum* to turn completely over by illuminating their under surfaces by means of a mirror.

In too bright light the transverse position of the leaves becomes changed to a position more or less in a line with the direction of the more intense light rays. In assuming a more perpendicular position to avoid the direct rays of the mid-day sun, the leaf-blades of *Lactuca Scariola* and the North American *Silphium laciniatum* necessarily take, according to STAHL, the direction of north and south, and so are often referred to as COMPASS PLANTS. A vertical position is also attained by the development of phyllodes, in connection with which may be mentioned the vertically placed leaves of many Myrtaceae and Proteaceae (82).

The heliotropic character of organs may change through the activity of external influences, and also at different stages of their development and growth. The flower-stalks of *Linaria cymbalaria* are at first positively heliotropic. After pollination, however, they become negatively heliotropic, and as they elongate they push their fruits into the crevices of the walls and rocks on which the plant grows (p. 257). The intensity of the illumination has a great influence, since plants which in subdued light are positively heliotropic exhibit negative heliotropism when the illumination is excessive. Between the two reactions a neutral aheliotropic condition exists. OLTMANNS, who elucidated this variation of the reaction with the intensity of the light, and the search for an optimal intensity which is connected with it (cf. heliotactic swarm-spores, p. 265), termed it PHOTOMETRY. It remains to be noted that it is not so much the absolute intensity of the light which is of importance, but that the degree of change in light intensity needed to alter the reaction of the plant depends on the illumination to which the latter has been previously exposed (83).

Heliotropic sensibility is markedly increased when traces of coal-gas, etc. are present as an impurity in the atmosphere. This is so strikingly the case that conclusions as to the degree of impurity can be drawn from the heliotropic deflection exhibited by susceptible plants (Peas, *Vicia calcarata*, etc.).

B. *Geotropism*

That the stems of trees and other plants should grow upwards and their roots downwards, is such a familiar occurrence and so necessary for the performance of their respective functions as to seem almost a matter of course. Just as in the discovery of gravitation 240 years ago, it required an especially keen spirit of inquiry to lead to the investigation of this everyday phenomenon. The fact that everywhere on the earth, stems take a perpendicular direction; and that, while buried in the earth, this same direction is assumed with certainty by germinating seeds and growing shoots; and chiefly the fact also that a shoot, when forced out of its upright position, curves energetically until it is again perpendicular, led to the supposition that the cause of these phenomena must be in a directive force proceeding from the earth itself. The correspondence in the behaviour of a stem in always assuming a perpendicular position, with the continued maintenance of the same direction by a plumb-line, suggested at once the force of gravitation, and the English investigator KNIGHT, in 1809, demonstrated that the attraction of gravitation, in fact, exerted an influence upon the direction of growth. As KNIGHT was not able to nullify the constantly operative influence of gravity upon plants and so directly prove its influence, he submitted them to the action of centrifugal force—an accelerative force operating like gravity upon the masses of bodies, which had, in addition, the advantage that it could be increased or diminished at will. KNIGHT made use of rapidly rotating, vertical wheels, upon which he fastened plants and germinating seeds in various positions. The result of his experiments was that the stems all turned towards the centre of the wheel and the roots directly away from it. On wheels rotating in a horizontal plane, where, in addition to the centrifugal force, the one-sided action of gravitation was also still operative, the shoots and roots took up an intermediate position depending on the combined influence of the two forces. In this way it was positively ascertained that terrestrial gravitation determines the positions of plant organs in respect to the earth ([84]).

Later, it was also shown that not only the perpendicular direction of stems and primary roots, but also the oblique or horizontal direction taken by lateral branches, lateral roots, and rhizomes, is due to a peculiar reaction towards the force of gravitation.

The property of plants to assume a definite position with respect to the direction of gravitation is termed GEOTROPISM. It is customary also, as in the case of heliotropism, to speak of positive and negative geotropism, diageotropism, and transverse geotropism, according to the position assumed by the plant or organ with respect to the centre of the earth. Still another form of geotropic irritability, lateral geotropism, renders possible the twining of stem-climbers.

Negative Geotropism.—All vertically upward growing organs, whether stems, leaves (Liliiflorae), flower-stalks, parts of flowers, or roots (such as the respiratory roots of *Avicennia* (Fig. 213), Palms, etc.), are negatively geotropic. In case such negatively geotropic organs are forced out of their upright position, they assume it again if still capable of growth. As in heliotropism, GEOTROPIC CURVATURE RESULTS FROM THE INCREASED GROWTH OF ONE SIDE AND THE RETARDED GROWTH OF THE OPPOSITE SIDE, and the region of greatest growth is, in general, also that of the greatest curvature. In negatively geotropic organs, growth is accelerated on the side towards the earth; on the upper side it is retarded. In consequence of the unequal growth thus induced, the erection of the free-growing extremity is effected. After the upright position is again attained, the one-sided growth ceases and the organ continues to grow in an upward direction.

The process of negative geotropic movement is dependent: (1) upon the vigour of the existing growth; (2) upon the sensibility of the organ; (3) upon the fact that the stimulus of gravity works most energetically when the apex of the orthotropic organ is removed about 90° from the vertical; the more nearly the zone capable of curvature approaches this position, the stronger is the motory stimulus; deviations from this optimal position of stimulation do not result in such striking differences in reaction as are caused by even very small ($\frac{1}{2}°$) deviations from the vertical; (4) and also upon the fact that after a stimulus has ceased to act upon a plant, the induced stimulation continues to produce so-called AFTER EFFECTS, just as by a momentary stimulus of light an after-perception persists in the eye.

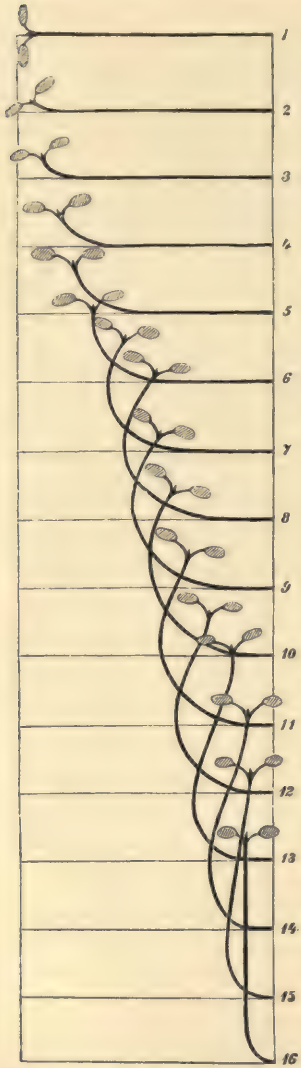


Fig. 225.—Different stages in the process of geotropic movement. The figures, 1-16, indicate successive stages in the geotropic curvature of a seedling grown in semi-darkness: at 1, placed horizontally; at 16, vertical. For description of intermediate stages see text. (Diagrammatic.)

These considerations determine the actual course of the directive movement of geotropism, which, as will be seen from the adjoining figure (Fig. 225), does not consist merely of a simple, continuous curvature. The numbers 1-16 show, diagrammatically, different stages in the geotropic erection of a seedling growing in semi-darkness and placed in a horizontal position (No. 1). The growth in the stem of the seedling is strongest just below the cotyledons, and gradually decreases towards the base. The curvature begins accordingly close to the cotyledons, and proceeds gradually down the stem until it reaches the lower, no longer elongating, portions. Through the downward movement of the curvature, and partly also through the after-effect of the original stimulus, the apical extremity becomes bent out of the perpendicular (No. 7), and in this way a curvature in the opposite direction takes place. Thus, under the influence of the stimulus, the stem bends backwards and forwards, until, finally, the whole growing portion becomes erect and no longer subject to the one-sided action of the geotropic stimulus.

Positive Geotropism is exhibited in tap-roots, in many aerial roots, and in the leaf-sheaths of the cotyledons of many Monocotyledons which penetrate the earth during germination. All these organs, when placed in any other position, assume a straight downward direction and afterwards maintain it. Formerly, it was believed that this resulted solely from their weight and the pliancy of their tissues. It is now known that this is not the case, and that positively geotropic, like negatively geotropic, movements are possible only through growth. The power of a downward curving root-tip to penetrate mercury (specifically much the heavier), and to overcome the resistant pressure, much greater than its own weight, proves conclusively that positive heliotropism is a manifestation of a vital process. Positive geotropic curvature is due to the fact that THE GROWTH OF AN ORGAN IN LENGTH IS PROMOTED ON THE UPPER SIDE, AND RETARDED, EVEN MORE STRONGLY, ON THE SIDE TURNED TOWARDS THE EARTH. A young root of the Chestnut, growing vertically, elongated equally on all sides 20 mm.; when placed horizontally, it exhibited a growth of 28 mm. on the upper and of only 9 mm. on the lower side. Fig. 226 illustrates the way in which the curvature takes place in the case of a root of the Broad Bean, which was marked at regular intervals with Indian ink and placed horizontally.

Diageotropism.—Most lateral branches and roots of the first order are diageotropic, while branches and roots of a higher order stand out from their parent organ in all directions. DIAGEOTROPIC ORGANS ARE ONLY IN A POSITION OF EQUILIBRIUM WHEN THEIR LONGITUDINAL AXES FORM A DEFINITE ANGLE WITH THE LINE OF THE ACTION OF GRAVITY. If forced from their normal inclination they return to it by curving. A special instance of diageotropism is exhibited by strictly horizontal organs, such as rhizomes and stolons, which, once they have attained their proper depth, show a strictly TRANSVERSE GEOTROPISM, and, if removed from their normal position, their growing tips always return to the horizontal. The oblique position naturally assumed by many organs is in part the result of other influences (epinasty and hyponasty, their own weight, and other directive forces).

A more complex form of geotropic orientation is manifested by dorsiventral organs, *e.g.* foliage leaves, zygomorphic flowers. All such dorsiventral organs, just as radial organs that are diageotropic, form a definite angle with the direction of gravity, but are only in equilibrium when the dorsal side is uppermost. If, in spite of the proper inclination of the longitudinal axis, the dorsal side should lie underneath, the latter elongates until it comes back again into a dorsal position.

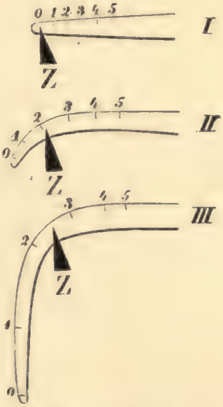


FIG. 226.—Geotropic curvature of the root of a seedling of *Vicia Faba*. *I*, Placed horizontally; *II*, after seven hours; *III*, after twenty-three hours; *Z*, a fixed index. (After SACHS.)

A state of torsion often results from the orientation movements of dorsiventral organs to recover from abnormal positions. Similarly, a torsion must also, of necessity, occur when a geotropic organ, which has become curved over toward its parent axis, turns itself about so as to face outwards (EXOTROPISM) (Fig. 227).

The rotation of the ovaries of many Orchidaceae, of the flowers of the Lobeliaceae, of the leaf-stalks on all hanging or oblique branches, of the originally reversed leaves (with the palisade parenchyma on the under side) of the Alstroemeriae, and of *Allium ursinum*, all afford familiar examples of torsion regularly occurring in the process of orientation (85).

Twining Plants.—In addition to the better-known forms of geotropism already mentioned, stem-climbers exhibit a peculiar geotropic movement, by means of which they are enabled to twine about upright supports. This movement depends upon the geotropic promotion of the growth of one side (not, as in negative or positive geotropism, of the upper or lower portions). Thus a geotropic curvature in a horizontal plane is produced (LATERAL GEOTROPISM), resulting in a revolving motion of the shoot apex. Twining plants occur in very different plant families; and although an upward growth is essential to their full development, their stems are not able of themselves to maintain an erect position. The erect stems of other plants, which often secure their own rigidity only through great expenditure of assimilated material (in xylem and sclerenchyma) are made use of by stem-climbers as supports, on which to spread out their assimilatory organs in the free air and light. The utilisation of a support produced by the assimilatory activity of other plants is a peculiarity they possess in common with other climbers, such as tendril- and root-climbers. Unlike them, however, the stem-climbers accomplish their purpose, not through the use of lateral clinging organs, but by the capacity of their main stems to twine about a support. The first internodes of young stem-climbers, as a rule, stand erect. By further growth the free end curves energetically to one side, and assumes a diageotropic, more or less oblique or horizontal position. At the same time the inclined apex begins to revolve in a circle either to the right or to the left. This is the movement which it has been customary to speak of as "revolving nutation," but which it is better to term REVOLVING MOVEMENT. The expression "nutation" is not in this case correct, as by it are understood autonomic movements; while THE REVOLVING MOVEMENTS OF STEM-CLIMBERS RESULT FROM THE EXTERNAL STIMULUS OF GEOTROPISM, which causes a promotion of growth in either the right or left side of the young internodes of the inclined shoot apex. As a result of this, a movement towards the other side is induced. On account of the direct connection of the apex of the shoot with the lower erect internodes, this revolving movement necessarily gives rise to a similar rotation of the revolving apex on its

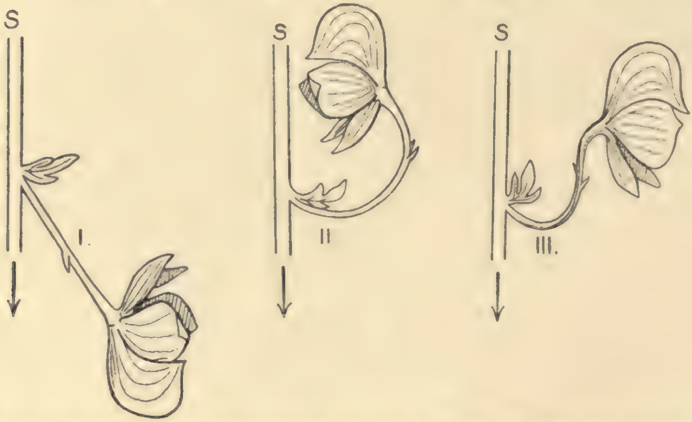


FIG. 227.—The movements by which a flower of *Aconitum napellus* regains its proper position when the axis bearing it (*S*) is inverted. *I*, Inverted position; *II*, position resulting from geotropism, the flower facing the parent axis; *III*, flower again facing outwards, after the exotropic movement.

longitudinal axis. Through this rotation the torsion, which would otherwise be produced by the revolving movement of the inclined tip of the shoot, is released. (This process will at once become apparent by imitating the movement with a rubber tube.) Thus the apex of a stem-climber sweeps round in a circle like the hands of a watch, and rotates at the same time like the axle to which the hand is attached. By this rotation of the shoot apex, the part of the stem subjected to the action of the lateral geotropism is constantly changing; and the revolving movement once begun, must continue, as no position of equilibrium can be attained.

Without the constant and unchanging action of gravitation in determining the direction of the revolving movement, the twining of a shoot continuously about a support is hardly conceivable. It is accordingly not without reason that the revolving movement is a continuous, fixed, geotropic movement, and not an autonomic nutation without definite directive force. Lateral geotropism is a physiological requisite for the climbing, and the existence of stem-climbers as such is dependent upon this peculiar form of geotropism. To this dependence, however, is also due the fact that stem-climbers can only twine about upright or slightly inclined supports. This is, it is true, a limitation to their power of climbing, but one which is not without advantage, for the plants are thus constrained to ascend to freer light and air (86).

When an upright support occurs anywhere in the immediate neighbourhood of the apex of a climbing shoot it is sure to be discovered. The apical extremity, the movement of which is but little disturbed by the leaves, which remain for a long time undeveloped, is forced by its lateral geotropism against the support, and by its next revolutions twines around it. If the support be thin, the coils, at first almost horizontal, are only loosely wound about it. Later they become more spiral, and so wind more tightly. This is accomplished by the ultimate predominance of negative geotropism in the coiled portions of the stem, which tends continually to draw out the coils and make the stems upright. This action of negative geotropism is well shown in the case of shoots which have formed free coils without a support. By the resistance offered by the supports to the complete elongation of the spiral stems, the shoots are held firmly in position. In many twining plants the roughness of their surfaces (due to hairs, bristles, hooks, furrows) also assists in preventing the shoots sliding down their supports. The autonomic torsion arising in the older portions of the stems is also of assistance in holding climbing plants, especially those with furrowed stems, tightly wound about their supports. The twining of stem-climbers, as well as the attachment to their supports, is thus due to geotropic processes of growth, and not, as in tendril-climbers, to contact stimuli. By the mechanism of their climbing process twining plants are restricted to moderately stout supports.

In addition to the autonomic torsions, a torsion from purely mechanical causes is necessarily manifested in the elongation of the coils of a twining stem, which are at first nearly horizontal, so far at least as it is not equalised by the free movement of the apex.

The direction of the revolving movements, and accordingly also of the windings, of most stem-climbers is constant. The twining stems are for the most part SINISTRORSE (*Convolvulus*, *Phaseolus*, *Pharbitis*, etc.). Seen from above, the windings run from the north towards the west, south and east to north again, *i.e.* just the reverse of the movement of the hands of a watch. Viewed from the side, the windings ascend the support from the left below to the right above (Fig. 228). DEXTRORSE stem-climbers with windings from east to west occur less frequently (Hop, Honeysuckle, *Polygonum convolvulus*, etc.). In the example chosen for illustration (*Myrsiphyllum asparagoides*, Fig. 229) the undeveloped condition of the lateral members in comparison with the elongated internodes of the stem is very apparent. A very few plants, such as *Blumenbachia lateritia*, *Hibbertia dentata*, and *Scyphantus*, seem able to climb equally well either to the right or to the left. A similar irregularity is shown in *Solanum dulcamara*, which, however, rarely twines, and then only under special circumstances.

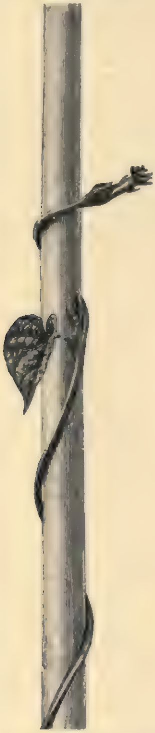


FIG. 228.—A sinistrorse stem-climber, *Pharbitis hispida*. The upper leaves remain small for a long time.

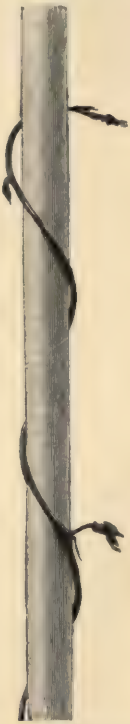


FIG. 229.—A dextrorse stem-climber. *Myrsiphyllum asparagoides*. The short lateral shoots have developed phylloeladia.

When the apex of a sinistrorse shoot points towards the north, it is the growth of the east side which is promoted by geotropism; in dextrorse climbers, on the contrary, the growth of the west side is more rapid. From the fact that the promotion of growth occurs always on the same side, it will be apparent that the apex of an inverted twining stem must unwind from its support (87). (Concerning the behaviour of stem-climbers on the klinostat compare p. 287).

Curvature of Grass-Haulms.—All the examples of geotropic movements, so far observed, took place in the growing portions of plants, and were due to a disturbance of the course of growth. A curvature even of lignified twigs can also be produced by the one-sided stronger growth of the cambium and of the young secondary tissues. Even many-year-old branches of Conifers are still able, although slowly, to exhibit geotropic curvatures ([88]). THE NODES OF GRASSES SHOW THAT RESTING TISSUES ALSO CAN BE EXCITED TO NEW GROWTH BY THE STIMULUS OF GRAVITATION. The knot-like swellings on the haulms of the Grasses are not nodes in a morphological sense, but are barrel-shaped thickenings of the leaf-sheaths above their actual insertion on the shoot axis. The part of the stem thus enveloped is very tender and flexible. When a grass-haulm is laid horizontally, which not unfrequently occurs through the action of the wind or rain, the nodes will begin to exhibit an energetic growth on their lower sides. As the upper sides of the nodes take no part in the growth, but are instead frequently shortened through pressure and loss of water, knee-like curvatures are formed at the nodes, by means of which the haulm is again quickly brought into an erect position (Fig. 230).

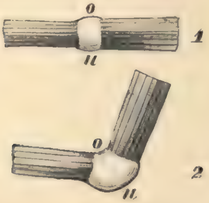


FIG. 230.—Geotropic erection of a grass-haulm by the curvature of a node. 1, Placed horizontally, both sides (u, o) of the node being of equal length; 2, the under side (u) lengthened, the upper side (o) somewhat shortened; as a result of the curvature the grass-haulm has been raised through an angle of 75°.

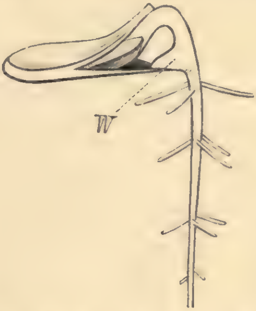


FIG. 231.—Seedling of *Cucurbita*. The peg (*W*) developed from the under side of the hypocotyl assists in rupturing the seed-coat.

Seedlings of Cucurbitaceae.—The stimulus of gravity induces the growth of a peculiar peg-like outgrowth from the lower side of the hypocotyl of the seedling of *Cucurbita* (Fig. 231 *W*). This peg, which results from a limited geotropic growth in thickness, assists in liberating the cotyledons from the seed-coat.

Modifications in the character of the geotropism, as of the heliotropism, of an organ may be occasioned by the operation of internal as well as external influences. Such changes in their geotropic position frequently occur, as VÖCHTING has demonstrated, during the development of flower-buds, flowers, and fruits, whose movements are, according to WIESNER, especially influenced by epinastic load-curvatures (p. 272). The burial of the fruits of *Trifolium subterraneum* and *Arachis hypogaea* is due to geotropism. Of the changes in the geotropic conditions of plant organs due to external causes, those are particularly noticeable which result from a failure of a sufficient supply of oxygen, by which, for example, roots and rhizomes are made negatively geotropic. The temperature influences the position of the main or lateral axes of many plants. Thus the stems of many spring plants, when the temperature is low, lie flat on the soil and only assume the erect position as the result of geotropism when the temperature becomes higher. Even more important are the modifications arising from the action of light, by which the geotropic irritability of rhizomes and foliage leaves may be so modified or weakened as to permit of more advantageous heliotropic positions.

While heliotropism was increased by the impurity of the atmosphere (p. 278), geotropism is weakened by this influence.

C. *Hydrotropism, Thermotropism, and other Tropisms*

While the illumination and the position with regard to the earth are the most general and important relations of the plant to its environment, and heliotropism and geotropism the most widely spread reactions of the plant, they are not the only phenomena of the kind. Whenever any external force or substance is important to the vital activity of a plant or any of its organs, there will also be found to be developed a corresponding irritability to their influences. Roots in dry soil are diverted to more favourable positions by the presence of greater quantities of moisture. The force of this POSITIVE HYDROTROPISM may be so great as to overcome the geotropic equilibrium of the roots, and thus give rise to hydrotropic curvatures. Conversely, the sporophores of many mould Fungi avoid moisture. To this property is due the fact, so advantageous for the distribution of the spores, that their sporangiophores grow directly away from a moist substratum. Corresponding to the chemotactic irritability of Bacteria and spermatozoids, roots, fungal hyphæ, and pollen tubes exhibit positive and negative CHEMOTROPIC CURVATURES. These vary according to the concentration of the solution, so that an attractive substance, at a higher concentration, may act repulsively. THERMOTROPISM or caloritropism (due to the stimulus of heat), RHEOTROPISM (occasioned by the direction of water currents), and AEROTROPISM (a form of chemotropism) are additional phenomena, which have been distinguished as arising from the special action of external stimuli, and stand in direct relations to certain vital requirements of plants (89).

In the case of ELECTROTROPISM, which has also been demonstrated in plants, no such essential relations have been discovered; the disposition of plant organs in a direction contrary to that of an electric current seems in no way to affect their well-being. The fact of the existence of electrotropism in plants shows clearly that an irritability may be present, from which no direct benefit is ordinarily derived, and which accordingly could not have been attained by natural selection.

D. *The Method of Slow Rotation—The Klinostat*

All the curvatures of growth previously discussed have been induced by the one-sided action of stimuli, the source of which determined the direction of the movements as well as the position of equilibrium. An influence operating equally on all sides is unable to produce a curvature in an organ of which the irritability is equally developed on all sides. In like manner no curvatures can take place when the plant is uniformly rotated, with a velocity sufficient to preclude the continuous operation of a stimulus on any one point long enough to occasion a one-sided growth. As in that case, no one side will be exclusively acted upon, but the growth of all will be equally promoted or retarded, the action of external influences, although exerted in only one direction, will be equalised. On this account the "method of slow rotation," originally instituted by SACHS, is of great assistance in the observation and investigation of the phenomena of movements. By means of it, heliotropic movements due to one-sided illumination may be prevented, without the necessity for either exposing the plants to the injurious effects of continued darkness or providing for an equal illumination on all sides. This method is, moreover, of especial value in investigating the movements due to the action of gravitation, for it is not possible to exclude its influence, as it is those arising from light, definite temperature, oxygen, etc.

WHEN PLANTS ARE SLOWLY ROTATED ON A HORIZONTAL AXIS THE ONE-SIDED ACTION OF GRAVITATION IS ELIMINATED, AND GEOTROPIC CURVATURE IS THUS PREVENTED in organs which react equally on all sides. The rotations are best produced by the KLINOSTAT, an instrument by means of which an exactly horizontal axis is rotated by clock-work. That geotropic curvatures of radial organs are, in fact, precluded by means of the klinostat, furnishes a remarkable corroboration of the result of KNIGHT'S experiments, and is a further proof that such curvatures are due to terrestrial gravitation. Through the equalisation of the action of external directive influences, radial portions of plants exhibit on the klinostat only such movements as arise from internal causes. The most important of these autonomic movements are those resulting in epinastic and hyponastic curvatures (p. 272), and the retrogression of recently formed paratonic curvatures through longitudinal extension (autotropism) or by curvature in the opposite direction (90).

Such autonomic movements should not be confused with those exhibited by dorsiventral organs on the klinostat, in consequence of the unequal irritability of their different sides. Through the special irritability of the dorsal side (p. 281) of foliage leaves and zygomorphic flowers, it is during their rotation more strongly acted upon by geotropic influence than the ventral side; as a result of this, curvatures are produced which so closely resemble those resulting from epinasty that they were for a long time actually considered as such (91). When stem-climbers are rotated on the klinostat, their revolving movement ceases, the part of the stem capable of growth unwinds and straightens, and afterwards exhibits only irregular nutations (92).

E. *Curvatures induced by Contact Stimuli*

The protoplasm of plants, like that of animals, exhibits an irritability to contact, whether momentary or continuous. This is apparent, not only from the behaviour of naked protoplasmic bodies, but also from the reactions manifested by walled cells and by whole organs, the functions of which may be so disturbed by the action of mechanical stimuli that death ensues. The almost universal irritability of vegetable protoplasm to mechanical stimulation is utilised by a number of plants for the production of movements which lead to their ultimate attachment to the irritating body. The mechanical stimulus is frequently perceived by means of special sense organs, the protoplasts of which are altered in shape owing to the contact. Tendril-climbers, in particular, have developed this irritability to contact stimuli as a means of attaching themselves to supports (cf. p. 67, Fig. 69); and in that way are enabled to elevate their assimilating and also their reproductive organs into more favourable situations. In the case of twining plants which possess similar powers of climbing, the process of elevation, as has already been shown, is accomplished by means of the geotropic irritability of the stems themselves. In the case of tendril-climbers, on the other hand, the attachment to the support is effected, not by the main axis of the plant, but by lateral organs of different morphological character. These may either maintain, at the same time, their normal character and functions, or, as is usually the case, become modified and as typical tendrils serve solely as climbing organs. According to FITTING, contact with a solid body quickly induces an increase in the growth of the opposite side of the organ, and this without any retardation of growth on the touched side leads to a sharp curvature of the tendril which coils it about the support. The more slender the tendrils and the stronger their growth, the more easily and quickly this process occurs. Through the tendency of the curvature to press the tendrils more and more firmly against the support, deep impressions are often made by them upon yielding bodies, soft stems, etc.

According to PFEFFER'S investigations, it is of great importance to the tendrils in the performance of their functions that they are not induced to coil by every touch, but only through CONTACT WITH THE UNEVEN SURFACE OF SOLID BODIES. Rain-drops consequently never act as a contact stimulus; and even the shock of a continued fall of mercury produces no stimulation, while a fibre of cotton-wool weighing 0·00025 mgr. is sufficient to stimulate the tendril (93).

In the more typically developed tendrils the curvature does not remain restricted to the portions directly subjected to the action of the contact stimulus. Apart from the fact that, in the act of coiling, new portions of the tendrils are being continually brought into contact with the support and so acted upon by the stimulus, the stimulation to curvature is also transferred to the portions of the tendril not in contact with the support. Through the action of the propagated stimulus, not only is the free apex of the tendril turned more quickly around the support, but a tendency to curvature is imparted to the portion of the tendril between the support and the parent shoot. As this is extended between two fixed points, this tendency causes it to coil spirally, like a corkscrew. With the spiral coiling, a torsion is produced, and since, on account of the fixed position of the two end points, it cannot be exerted in one direction only, the spiral, for purely mechanical reasons, coils partly to the left and partly to the right. POINTS OF REVERSAL (*x*) thus occur in the windings which, in equal numbers to the right and to the left, equalise the torsion (Fig. 232). By the spiral coiling of the tendrils the parent-stem is not only drawn closer to the support, but the tendrils themselves acquire greater elasticity and are enabled to withstand the injurious effects of a sudden shock.

Advantageous changes also take place in the anatomical structure of the tendrils after they are fastened to the supports. The young tendrils, during their rapid elongation, exhibit active nutations, and thus the probability of their finding a support is enhanced. During this time they remain soft and flexible, while the turgor rigidity of their apices is maintained only by collenchyma. In this condition they are easily ruptured, and have but little sustaining capacity. As soon, however, as a support is grasped, the coiled-up portion of the tendril thickens and hardens, while the other part lignifies, and becomes so strengthened by sclerenchymatous formations that the tendril can finally sustain a strain of many pounds. When the tendrils do not find a support they usually dry up and fall off, but in some cases they first coil themselves into a spiral.

The tendrils of many plants (*Cobaea*, *Eccremocarpus*, *Cissus*) are irritable and capable of curving on all sides ; others (tendrils of Cucurbitaceae and others with hooked tips) are, according to FITTING, sensitive on all sides but only curve when the under side is touched ; if the upper surface is at the same time stimulated curvature is arrested. In some cases the tendrils quickly grasp the support (*Passiflora*, *Sicyos*, *Bryonia*) ; while in other tendrils the supports are very slowly grasped (*Smilax*, *Vitis*).

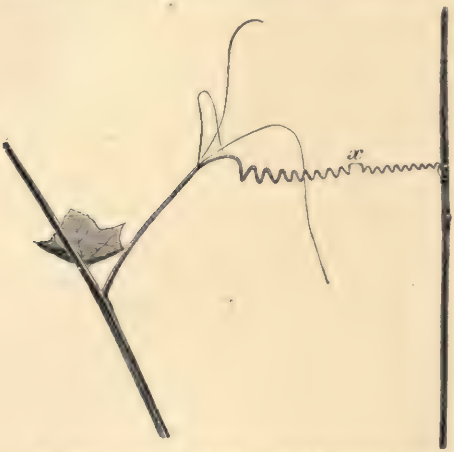


FIG. 232.—Portion of a stem of *Sicyos angulatus* with tendril ; *x*, point of reversal in the coiling of the tendril.

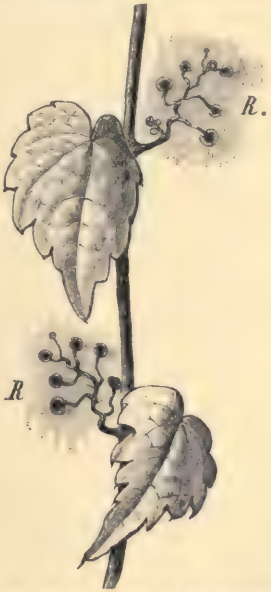


FIG. 233.—Portion of a climbing shoot of *Ampelopsis Veitchii.* The tendrils (*R*) have fastened themselves to a smooth wall by means of holdfasts.

Tendril-climbers are not, like twining plants, restricted to nearly vertical supports, although, on account of the manner in which the tendrils coil, they can grasp only slender supports. A few tendril-climbers are even able to attach themselves to smooth walls. Their tendrils are then negatively heliotropic, and provided at their apices with small cushion-like outgrowths, which may either develop independently on the young tendrils, or are first called forth by contact irritation. Through their sticky excretions these cushions become fastened to the wall and then grow into disc-like suckers, the cells of which come into such close contact with the supporting wall that it is easier to break the lignified tendrils than to separate the hold-fasts from the wall. Fig. 233 represents the tendrils of *Quinaria* (*Ampelopsis*) *Veitchii.* The suckers occur on its young tendrils in the form of knobs. In *Quinaria quinquefolia* and *Qu. radicantissima* the suckers are only produced as the result of contact, and the tendrils of these plants are able also to grasp thin supports.

Sometimes, as in the case of *Lophospermum scandens* (Fig. 234), the leaf-stalks, although bearing normal leaf-blades, become irritable to contact stimuli and function as tendrils. Of leaf-stalks which thus act as tendrils, good examples are afforded by *Tropaeolum*, *Maurandia*, *Solanum jasminoides*, *Nepenthes*, etc. The subsequent modifications occurring in more perfectly developed tendrils are not noticeable in the case of petiolar tendrils, although the coiling portion of the leaf-stalk of *Solanum jasminoides* does become strongly thickened and lignified; while the leaf-blades of *Clematis*, by remaining small for a time, enhance the tendril-like character of their leaf-stalks, and by bending backwards also assist in maintaining the initial contact with a support. At other times the midribs of the leaf-blades themselves become prolonged, and assume the function of tendrils (*Gloriosa*, *Littonia*, *Flagellaria*). In many species of *Fumaria* and *Corydalis*, in addition to the leaf-stalks, even the leaf-blades of the leaflets twine around slender supports, while the parasitic shoots of *Cuscuta* (Fig. 186) are adapted for both twining and climbing. Climbing parts of the thallus occur in some Thallophyta (Florideae) (94).

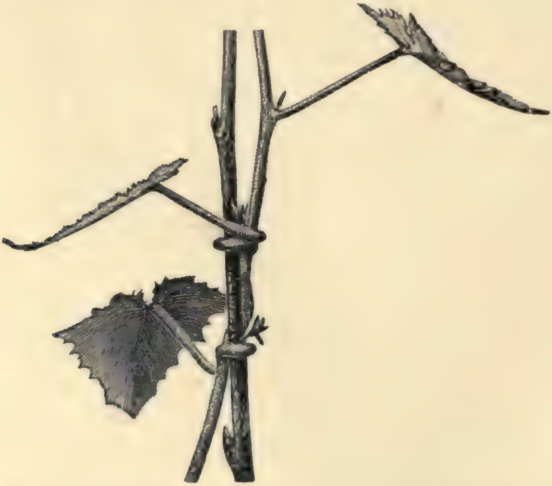


FIG. 234.—*Lophospermum scandens* climbing by means of its tendril-like petioles.

F. *Curvatures of Growth due to Variations in Light and Temperature*

The flowers and foliage leaves of many plants exhibit the peculiarity that their different sides (the upper and under sides of foliage-leaves and leaf-stalks, the inner and outer sides of floral leaves) show an unequal growth in response to even transitory and slight variations in temperature and in the intensity of light. Whenever, on account of such variations, the growth of the under side of a leaf exceeds that of the upper side, the whole leaf moves upwards and towards the parent axis; while if the growth of the upper side is the stronger, the leaf is depressed.

Movements of this nature are especially noticeable in flower-leaves, and bring about the opening and closing of the flower. A rise of temperature causes the flowers of the Tulip and Crocus, and also those of *Adonis*, *Ornithogalum*, and *Colchicum*, to open, while sudden cooling causes them to close. Tulips and Crocuses, if brought, while still closed, into a warm room, open in a very short time; with a difference of temperature of 15°-20° C., in from two to four minutes. Crocuses respond to an alteration in temperature of ½° C.; Tulips to a variation of 2°-3° C. In warm sunshine the spring or summer flowers are open for the visits of insects, but on a lowering of temperature the sexual organs are covered up and protected.

The flower-heads of *Taraxacum*, *Leontodon*, and other Composites, also the flowers of *Nymphaea*, *Cacti*, etc., open when illuminated, and close when kept in darkness (Fig. 235).

Variation of light produces also unequal growth in foliage-leaves, particularly in those of the Chenopodiaceae, Caryophyllaceae, and Balsaminaceae, and cause them to assume so-called SLEEP POSITIONS.

In many instances the movements of the floral leaves are produced by variations of light as well as of temperature; for example, some of the flowers mentioned open in the light and close in the dark, although the temperature remains constant. In the case of opposing external influences, the resulting direction of the movement of the flower-leaves is determined by the influence which is predominant. The dependence of these movements upon different, and often opposing, influences, together with the continuance of movements induced by previously operative influences, led to their being for long misunderstood, especially as the movement of opening is from internal causes followed by a closing movement even if a high temperature is maintained (95).

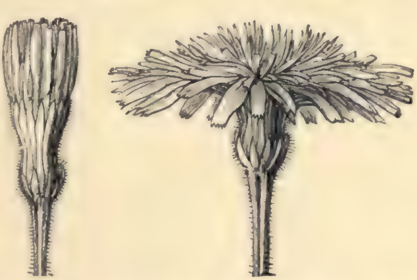


FIG. 235.—Flower-head of *Leontodon hastilis*, closed when kept in darkness, open when illuminated. (From DETMER'S *Physiol. Pract.*)

These movements, occasioned by variations in the illumination and temperature, must not be confused with those of heliotropism and thermotropism; in both of which the movement induced in an organ is dependent upon its relative position with respect to the source of the light or heat, and not upon the varying intensity of the stimulus. The movements last discussed are photonastic or thermonastic, *i.e.*, they result from the variation in illumination or temperature, and not from the direction of the light or heat rays.

3. Movements due to Changes of Turgor (Variation Movements)

The various movements hitherto considered are, to a large extent, the result of the action of forces acting on growth. These movements were therefore confined to organs, or parts of organs, still in a state of growth. In contrast to the almost universal immobility of all fully-grown organs, it is interesting to find that some plants have found a means of carrying on vigorous movements without the assistance of growth.

It has already been shown (p. 179) that through the pressure of increasing turgidity the elastic cell walls become greatly distended and the cell cavity expanded, while, on the other hand, the cell walls shrink and the cell becomes smaller when the turgor is diminished (Fig. 174). It is to these changes in volume, which thus result from alterations in turgor, that the varying movements of fully developed living organs are due.

Such variation movements occur only in foliar organs (foliage and flower leaves, stamens, style and stigmatic lobes). These movements are especially noticeable in the compound leaves of the Leguminosae and Oxalideae, and also in the leaflets of *Marsilia*. In the motile regions of these leaves special masses of tissue are, both physiologically and anatomically, adapted for the promotion of this form of movement.

This tissue appears externally as a firm cushion or PULVINUS, sharply distinguished from the rest of the leaf-stalk, and is the direct cause of the leaf movements. Anatomically considered, the pulvinus consists, for the most part, of strongly turgescent parenchyma with very elastic cell walls. The vascular bundles and mechanical elements, which, in other portions of the leaf-stalk, are situated towards the circumference, unite in the pulvinus in the form of a single flexible strand, and so offer little opposition to the movement of the leaf resulting from the curvature of the motile region (p. 182). The unfavourable arrangement of the mechanical tissues is compensated by the turgescence of the parenchymatous tissues on which the support of the leaf-blade in its proper position in these cases depends. The parenchyma of the pulvinus forms a thick enveloping layer about this axial strand, by means of which, through the pressure arising from a difference in the turgescence of its opposite sides, a movement of the whole leaf-blade is brought about, similar to that of the outspread hand by the motion of the wrist.

These variation movements are either autonomic, when the variations of turgor are due to no recognisable external influence, or paratonic (aitionomic), when the turgor is regulated in a definite way by the action of external stimuli.

Autonomic Variation Movements.—A remarkable example of this form of movement is furnished by the small lateral leaflets of *Desmodium* (*Hedysarum*) *gyrans*, a papilionaceous plant growing in the damp Ganges plains and still more strikingly, according to MOLISCH, by *Oxalis hedysaroides*. In a moist, warm atmosphere (22°-25°) these leaflets make circling movements which are in no way disturbed by variations in the intensity of the light, and are of such rapidity that the tips describe a complete circle in 1-3 minutes; in the case of the leaflets of *Oxalis* a path of ½-1½ cm. is traversed in one or a few seconds. Variations in illumination do not disturb these movements. The autonomic variation movements of *Trifolium* and of the Wood-Sorrel take place, on the contrary, only in darkness. Thus the terminal leaflets of *Trifolium pratense* exhibit oscillatory movements in the dark with an amplitude which may exceed 120°, and are regularly repeated in periods of 2-4 hours; but on exposure to light the leaflets cease their oscillations and assume a fixed light position.

Paratonic Variation Movements are chiefly induced by variation in the intensity of the light, by the stimulus of gravitation, and by mechanical irritation (shock, friction). The pulvini of leaves may be affected by several different stimuli; the leaves of *Mimosa pudica*, for example, are set in motion by the action of light, by the stimulus of a shock, and sometimes also by gravitational stimuli; in addition they exhibit autonomic movements.

A change from light to darkness, as from day to night, occasions NYCTITROPIC MOVEMENTS or the so-called SLEEP MOVEMENTS. In the day or light position, which is the same as that of diaheliotropic foliage-leaves, the leaf-blades are perpendicular to the incident rays of light. With the commencement of darkness the leaves or the single leaflets fold either upwards with their upper surfaces inward, or downwards with their lower surfaces together, and so remain until the diurnal position is again assumed on recurring illumination. THE VARIATIONS IN TURGESCENCE IN THE OPPOSED HALVES OF THE JOINT STAND IN INVERSE RELATION TO ONE ANOTHER; OR IF OF THE SAME NATURE ARE UNEQUAL IN DEGREE (96).

As sleep movements are also manifested by plants growing in tropical climates, where no injurious nocturnal fall of temperature occurs, the purpose of the sleep position suggested by DARWIN, viz. the protection of the leaves from excessive cooling, does not hold in all cases. STAHL seeks it also in the lessening of the formation of dew, and the more energetic transpiration of the unwetted leaves which would result. Sleep movements are particularly noticeable in *Phaseolus*, *Trifolium*, *Robinia*, *Acacia lophantha*, *Amicia zygomeris* (Fig. 236), *Mimosa pudica*, *Oxalis*, *Marsilia*, *Porlieria*; while less striking movements take place in many other plants.

Too intense light frequently causes the change from the diurnal position, and a movement either towards or away from the nocturnal position. The leaflets of the common Locust (*Robinia pseudacacia*) are folded downwards at night. In ordinary diffuse daylight they assume their diurnal, outspread position; but, if exposed to the direct rays of the mid-day sun, they turn obliquely upwards. In many plants ALTERATIONS IN THE INTENSITY OF THE LIGHT ALTER THE GEOTROPISM OF THE MOTILE ORGANS; the sleep movements are then accomplished by the help of geotropic variation movement (*Phaseolus*, *Lupinus*) (97).

The change from the diurnal to the nocturnal position continues for a time to take place, even in constant darkness or prolonged illumination. The leaves themselves seem to have a tendency to pass at regular intervals from one condition to the other. The daily periods are the result of the stimulus imparted by the light, the periodic action of which induces the regular changes of position.

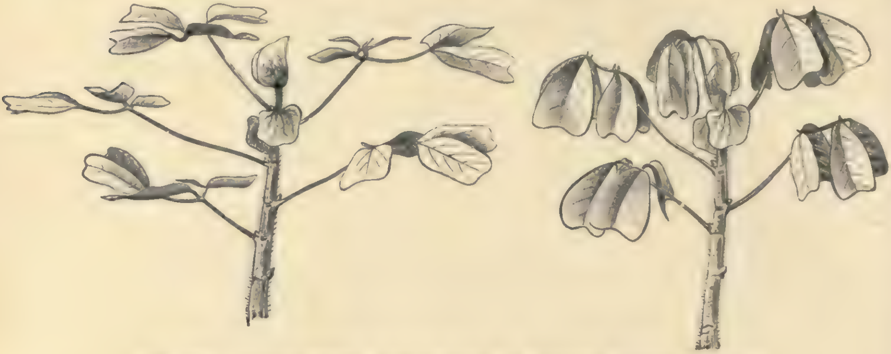


FIG. 236.—*Amicia zygomeris*, showing diurnal and nocturnal position of leaves.

If, however, the external stimulus ceases to operate, the internal disposition still continues for some time to give rise to visible after-effects (p. 261), until finally, from the abnormal conditions, an abnormal state of rigor (light rigor, dark rigor) and symptoms of disease are manifested (⁹⁸).

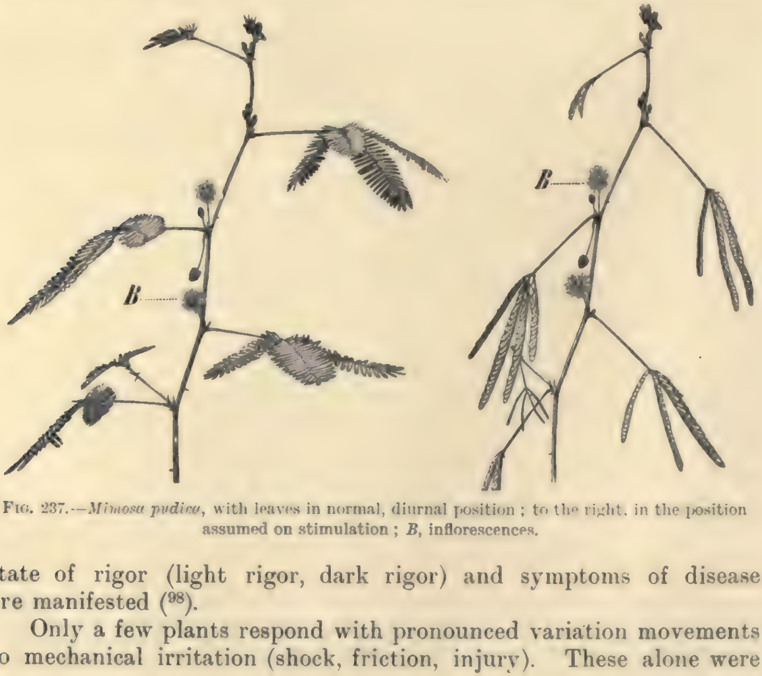


FIG. 237.—*Mimosa pudica*, with leaves in normal, diurnal position; to the right, in the position assumed on stimulation; *B*, inflorescences.

Only a few plants respond with pronounced variation movements to mechanical irritation (shock, friction, injury). These alone were considered irritable plants, so long as only mechanical irritations, from which visible movements resulted, were regarded as stimuli.

Of irritable plants in this sense, mention has already been made of *Dionaea muscipula* (p. 237), whose leaves, when touched on the upper side, especially if the bristles are disturbed, fold together. The most familiar example of this irritability to mechanical stimuli is furnished by *Mimosa pudica*, a tropical leguminous shrubby plant, which owes its name of sensitive plant to its extreme sensitiveness to contact. The leaves of this plant are doubly compound (Fig. 237). The four secondary leaf-stalks, to which closely crowded leaflets are attached left and right, are articulated by well-developed pulvini with the primary leaf-stalks; while they, in turn, as well as the leaflets, are similarly provided with motile organs. Thus all these different parts are capable of independent movement, and the appearance of the entire leaf becomes, in consequence, greatly modified. In their unirritated, light position (Fig. 237, on the left) the leaf-stalk is directed obliquely upwards, while the secondary petioles with their leaflets are extended almost in one plane. Upon any vibration of the leaf, in favourable conditions of temperature (25°-30° C.) and moisture, all its parts perform rapid movements. The leaflets fold together, and, at the same time, move forward, the secondary petioles lay themselves laterally together, while the primary leaf-stalk sinks downwards (Fig. 237, on the right). Leaves thus affected, if left undisturbed, soon resume their former position.

The behaviour of the leaves is still more remarkable when only a few of the leaflets are acted upon by the stimulus. This is easily demonstrated by holding a burning match near the leaflets of one of the pinnæ. The leaflets directly affected by the flame fold quickly upwards, and this movement is performed successively by each pair of leaflets of the pinna until the articulation with the primary leaf-stalk is reached. The stimulation is then conveyed to the other pinnæ, the leaflets of which go through the same movement in a reverse order; finally, the secondary petioles themselves draw together. Suddenly, when the whole process seems apparently finished, the main leaf-stalk in turn makes a downward movement. From this leaf the stimulus is able to travel still farther through the stem, and it may thus induce movement in leaves 50 cm. distant.

The movements of the pulvini are due solely to differences in turgidity which, as in the case of nyctitropic movements, occur antagonistically in the halves of the pulvinus. It has been observed that a sudden escape of water into the intercellular spaces takes place out of the cells of the lower or irritable side of the pulvinus of the primary leaf-stalk; the lower surface is that provided with tactile hairs. According to the investigations of HABERLANDT, the conduction of the stimulus does not appear to be accomplished by the movement of the water thus discharged, but by the mucilaginous contents of tubular cells which are situated in the phloem portion of the vascular bundles; while FITTING regards the conduction as taking place through living cells. MACDOUGAL was unable to induce the movements by causing differences in the hydrostatic pressure. The position of an irritated leaf resembles externally its sleep or nocturnal position, but in reality the turgor tension of the pulvinus is different [99].

Neptunia oleracea, *Desmanthus plenus*, and *Biophytum sensitivum* are similar though less sensitive. *Robinia pseudacacia* and *Oxalis acetosella* respond to violent mechanical stimuli by slight but similar movements.

The state of rigor sometimes occurring in motile organs may also be best observed in *Mimosa*, for, although so sensitive to the action of external influences, it does not exhibit its irritable movements at all times. Whenever the temperature of the surrounding air falls below a certain level, no movements take place, and the whole plant passes into a condition known as COLD RIGOR, while, on the other hand, at a temperature of about 40°, HEAT RIGOR occurs. DROUGHT RIGOR is induced, just before withering, by an insufficient supply of water, and a DARK RIGOR by a prolonged retention in darkness, probably owing to the derangement of the chloroplasts. In a vacuum, or on exposure to hydrogen and other gases—chloroform vapour, coal gas, etc.—movement also ceases, partly on account of insufficient oxygen, and partly from the actual poisonous action of the gases themselves. If the state of rigor is not continued too long, the original irritability will again return on the restoration of normal conditions ([100]).

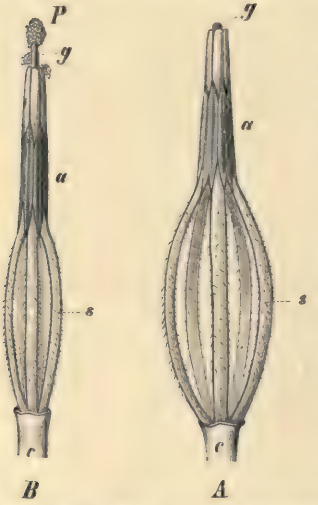


FIG. 238.—A single flower of *Centaurea jacea* with perianth removed. *A*, stamens in normal position; *B*, stamens contracted; *c*, lower part of tubular perianth; *s*, stamens; *a*, anther-tube; *g*, style; *P*, pollen. (After PFEFFER, enlarged).

The movements of irritability exhibited by the staminal leaves of some Berberidaceae (*Berberis, Mahonia*) and Compositae (Cynareae and Liguliflorae) bear a certain relation to those of foliage leaves. The bow-shaped filaments of the stamens of the Compositae straighten upon mechanical irritation. As they frequently contract 10-20 per cent of their length, the style becomes extended beyond the anther-tube (Fig. 238). The reduction in the length of the filaments is accompanied by a moderate increase in their thickness, due to the elastic contraction of the cell walls, and the consequent expulsion of water into the intercellular spaces. The stamens of *Berberis* and *Mahonia* are only sensitive to contact on the inner side near their base, and as their contraction occurs only on the inner side, the anthers are thus brought into contact with the stigma ([101]). Examples of variation movements of carpellary leaves may be seen in the flowers of *Mimulus, Strobilanthes* (*Goldfussia*), *Martynia, Torenia,* and other plants. The two lobes of the styles of these flowers fold together when irritated. The stigmas of *Mimulus* and *Torenia* open again shortly unless active pollen has been deposited when they remain in the closed condition. Similarly, in the flowers of *Stylidium*, a sudden upward movement of the bent style occurs when it is irritated by a touch.

VI. Reproduction

The life of every plant is of limited duration. Death ensues, sooner or later, and the decayed remains form a part of the surface soil. All existing plants are descended from ancestral forms. A spontaneous generation of new organisms from lifeless matter does not, as far as experience teaches, take place, and all existing vegetable life owes its existence to the capacity inherent in all organisms of reproducing their kind. Reproduction is accordingly a vital power which must be exercised by every existing plant species.

It is also evident from the very nature of reproduction that in the production of new organisms a process of rejuvenation is continually being carried on. The descendants commence their development at a stage long since passed over by the parents.

The formation of independently existing offspring necessitates also their separation from the parent plant. The formation of a new bud by a tree is not distinguished as reproduction so long as the bud remains in connection with the tree as a part of the whole. But if the bud became separated from the tree and continued its existence as an independent plant, that would constitute a form of reproduction, and, in fact, this actually takes place in many plants.

The conditions of the outer world make the still further demand upon reproduction, that from it a multiplication of the species should result. As the germs after separation from the mother plant do not always find the conditions necessary for their development and so, for the most part, perish, the extinction of the whole species would soon result if a plant produced but a single germ. That in reproduction care is taken for the multiplication of the individual in an almost spendthrift manner, is shown by a consideration of the innumerable spores produced by a single mushroom, or by a large fern. **Bessey** has estimated the number of seeds produced annually by a Poplar tree at about 28 millions.

Rejuvenation, separation, and multiplication of the individual are accordingly the essential requisites of reproduction.

These requirements are fulfilled by plants in the most varied manner. Each great division of the vegetable kingdom has adopted its own special method; and each family and genus, or even the different species, are characterised by some peculiar feature of their manner of reproduction. Systematic botany is, indeed, essentially based upon differences in the development of the reproductive organs and in their functions.

Numerous and varied as the processes of reproduction in the vegetable kingdom are, they are in reality but modifications of two different and distinct modes of reproduction.

The simpler of these, or vegetative reproduction, consists in the formation of cells or cell-bodies which, after their separation from the parent plant without undergoing any further change, either germinate at once, or develop into new organisms after a period of rest. This mode of reproduction, in which the growth and development of the parent plant are directly continued, is also distinguished as MONOGENETIC, VEGETATIVE, or ASEXUAL reproduction. The special peculiarities and laws of growth of the parent plant are in this case directly transmitted to the offspring.

In SEXUAL REPRODUCTION, the second of the two modes of reproduction, two kinds of reproductive cells each of which carries the characters of the organism producing it are first formed, but neither is directly capable of further development, and both perish in a very short time, unless opportunity is given for their fusion with each other. Not until one cell (the female) has fully taken up and become inseparably united with the other cell (the male), does it acquire the capacity of development and growth. This mode of reproduction is designated SEXUAL or DIGENETIC reproduction.

The physiological significance of sexual reproduction is not at once apparent. In many plants the vegetative mode of reproduction is sufficient to secure the necessary multiplication of the species, so that plants are able to continue without sexual reproduction. Many Fungi, for instance, are reproduced only vegetatively; the cultivated Banana, many Dioscoreaceae, and varieties of the Grape, Orange, and the Strawberry, no longer reproduce themselves sexually, but are propagated solely in a vegetative manner. The Garlic, which forms small bulbs in place of flowers, the White Lily, and *Ranunculus Ficaria*, which reproduces itself by root tubers, are hardly able to produce good seeds, which can, however, be obtained by operative interference, *e.g.* on separated inflorescences. They multiply exclusively by asexual methods without suffering any degeneration. Continued reproduction by vegetative means used to be regarded as necessarily injurious (102).

Since monogenetic reproduction is sufficient for the preservation of the species, sexual reproduction must answer some purpose not attained by the vegetative mode of multiplication, for otherwise it would be altogether superfluous that the same plant, in addition to the vegetative, should also possess the sexual form of reproduction, which is so much more complicated and less certain. Even the common Moulds, whose vegetative spores (conidia) are very widely distributed, occasionally develop sexual reproductive cells in specially formed sexual organs.

In many of the lower plants (Algae and Fungi) it has been shown that the development of sexual cells is dependent upon definite external influences. KLEBS has demonstrated, in fact, that it is possible by regulation of the external conditions (nutrition, temperature, transpiration, composition of substratum and of the surrounding medium) to induce them to produce at will either non-sexual swarm-spores or sexual cells. In many plants unfavourable external conditions apparently give the impetus to a sexual mode of reproduction. The sexual product (zygospores of Algae, Phycomycetes) seems better able than the vegetative germs (swarm-spores of Algae, conidia) to remain a long time at rest, and so withstand the disastrous effects of an unfavourable environment. No inference can be drawn, however, from the function of the sexual germs in this instance concerning the necessity for the existence of a sexual, in addition to a vegetative, mode of reproduction; for in other cases it is the vegetative reproductive bodies, as, for example, the spores of Ferns, which are especially equipped for a period of enforced rest (103).

What makes digenetic reproduction essentially different from monogenetic is the UNION OF THE SUBSTANCES OF THE PARENTS AND THE CONSEQUENT TRANSMISSION AND BLENDING OF THE PATERNAL AND MATERNAL PROPERTIES.

It is in this qualitative influence that the chief difference between sexual and vegetative reproduction is shown. And this may be regarded as the special advantage of sexuality. BY VEGETATIVE REPRODUCTION THE QUANTITATIVE MULTIPLICATION OF THE INDIVIDUAL IS SECURED, WHILE BY SEXUAL REPRODUCTION A QUALITATIVE INFLUENCE IS EXERTED. THE VEGETATIVELY PRODUCED PROGENY CONSIST OF UNMIXED DESCENDANTS; THE SEXUALLY PRODUCED OFFSPRING, ON THE OTHER HAND, ARE THE RESULT OF A BLENDING OF THE PARENTS.

In vegetative multiplication the complex of properties unfolded in the descendants does not as a rule differ from that possessed by the parent form. By vegetative multiplication all the varieties and races of cultivated plants, the characters of which do not come true by seed, are maintained. Variation may, however, occur among the vegetatively produced progeny. The occurrence of this may be compared to bud-variation, in which a single bud on a tree may give rise to a branch deviating in colour and form from the type; such a bud-variation may, years after, return suddenly to the characters of the typical form. In the same way variations arise among vegetatively produced plants, a remarkable example of which, according to BEYERINCK, is afforded by the Bacteria, the reproduction of which takes place exclusively by division into two (104).

The sexually produced offspring, on the other hand, endowed with the properties of the father, can never be identical with the mother-plant, but possess the properties of both parents. When these are divergent they frequently play very different parts in the descendants, some (dominant) characters appearing conspicuously, while others (recessive characters) become less marked or remain completely latent. In this way the descendants do not exhibit a uniform mean between the parents, but some may resemble the father, others the mother. These relations determine the character of the sexually produced descendants (cf. p. 313 ff.). Variations appearing in single individuals will, unless they are of an absolutely dominating character, become modified and ultimately lost by crossing with ordinary individuals. In such a case sexual reproduction tends to maintain the constancy of the species. In other cases, as when one parent possesses new and dominant characters or when both parents tend to vary in the same direction, the deviation from the ancestral form may be maintained or increased by sexual reproduction.

The great tendency to variation commonly exhibited by hybrids (p. 313) illustrates how the equilibrium of the complex of properties of a sexually produced individual is affected by divergent parental tendencies. But, even as a result of ordinary fertilisation, not only small and readily disappearing variations (fluctuating variations) but sometimes more striking ones occur, in which the offspring differs so strongly from the parents in characters, which can be inherited, that it appears to be a new species or sub-species. Of such *petites espèces* of *Draba verna* some two hundred are known. In such sudden variations (the occurrence of which v. KÖLLIKER, and with him KORSCHINSKY, term heterogenesis, while DE VRIES more recently calls it mutation) these authors seek the starting-points of the origin of new species. This would occur when a particular species passes, from unknown causes, into a period of mutation such as DE VRIES demonstrated experimentally in *Oenothera Lamarckiana*. KORSCHINSKY collected a number of historical examples of heterogenesis, of which *Chelidonium laciniatum*, which appeared in a garden at Heidelberg in 1590, and *Capsella Heegeri*, SOLMS, which only recently appeared, will serve as examples (^{105}).

The fluctuating variations which largely determine the valuable characters of economic plants (*e.g.* the high percentage of sugar in the Sugar Beet) are in contrast to the mutations not fixed on inheritance. Careful and continued selection of the varying progeny is thus necessary to maintain the required standard of the race.

The experience of cultivators and the recent experimental work on lower plants carried out by KLEBS show that different groupings of the internal and external conditions of life favour reproduction and ordinary growth respectively. In fact growth and reproduction frequently though not always appear to be mutually exclusive.

Vegetative Reproduction

Vegetative reproduction, the purely quantitative character of which as a mere process of multiplication has been emphasised, exists generally throughout the vegetable kingdom, and but few plants, *e.g.* some of the Conifers and Palms, are altogether devoid of it. Mention has already been made in considering artificial propagation that, from the separate parts or single cells, or even from the naked protoplasts (Siphoneae) of many plants, the regeneration of a new and perfect individual may ensue. In vegetative reproduction the process is similar except that the separation of the part from the parent plant is an organic one, occurring in the natural course of development. The vegetative form of reproduction is manifested in various aspects, and may be distinguished as a multiplication by means of multicellular vegetative bodies (buds, gemmæ), or by single cells (spores).

Multiplication by Multicellular Vegetative Bodies (Budding) often consists merely in the separation of lateral shoots, or in a division of a single plant into several. In this way the lateral shoots of *Azolla*, through the death and disruption of the older parts of the parent axis, become separated from one another and continue their growth as independent plants; similarly, separate plants originate from the vegetative body of the Duckweed (*Lemna*).

Multiplication by stolons, rhizomes, and tubers results in a similar formation of independently existing plants. As may be seen in the Strawberry, the Bugle (*Ajuga reptans*) and numerous other plants, the shoots produced from many of the axillary buds of the widely outstretched stolons take root and form new plants. In cases where the runners themselves eventually die, the parent plant becomes finally surrounded by a colony of entirely independent plants. Instead of forming runners, the single tuber may divide (*Corydalis solida*), and in this way give rise to two, four, or more new tubers. New bulbs are produced in the leaf-axils of the bud-scales of bulbs, while brood buds (bulbils, gemmæ) are frequently developed on aerial vegetative organs.

Bulbils are found on the inflorescence in the place of the flowers in many species of *Allium*, in the grass *Poa bulbifera*, and also in *Polygonum viviparum*. In *Lilium bulbiferum*, *Dentaria bulbifera*, etc., the bulbs in the axils of the leaves are specially constructed with a view to detachment from the parent plant (Fig. 22). The swollen leaves contain reserve food material, and frequently develop roots before falling from the plant. In *Ranunculus Ficaria* the roots of the axillary buds are full of reserve food material, and resemble grains of corn. When the plant dies the bulbils remain on the ground, and have given rise to the fable of showers of grain. Bulbils or gemmæ are met with also among the Mosses, Liverworts, and Ferns. The winter buds of many water plants (*Hydrocharis*, *Utricularia*, *Lemna*, etc.) have a peculiar biological significance. They are formed in the autumn, and sink to the bottom of the water; in the succeeding spring they rise to the surface and form new plants.

By vegetative multiplication higher plants can annually give rise to individuals which are strong and capable of flowering and fruiting. The seedlings of such plants, on the other hand, often require to grow for several years before the capacity of sexual reproduction is attained (bulbous plants, Hop, etc.).

In addition to the instances just cited, in which the vegetative reproductive bodies take their origin from points where lateral shoots are normally formed, they may also appear in places where no shoots are normally developed. Thus the adventitious formations often found on leaves, particularly on the leaf-blades, serve the purpose of reproduction. Just as the leaves of *Begonia*, *Drosera*, etc., after they have been cut off, are able to give rise to new plants, in other cases the leaves possess this power while still growing on the parent plant. Some ferns afford specially characteristic examples of this (*Asplenium decussatum*, *A. Fabianum*, *A. bulbiferum*, *A. viviparum*) ; adventitious buds are produced on their laminæ, developing into small rooted plants, which then fall off and complete their development (Fig. 239). The adventitious buds of *Cystopteris bulbifera* take the form of bulbils with small swollen leaves. Adventitious plantlets are frequently formed also on the leaves of *Cardamine pratensis*, and *Cardamine amara* manifests a similar tendency. One of the best-known examples of such adventitious formations is afforded by the leaves of the tropical *Bryophyllum*, in the marginal indentations of which the brood plantlets develop in great numbers. Even the force of the wind is sufficient to detach the leaflets of *Bryophyllum* from the plant. Gemmae are abundantly produced on the thallus of many Hepaticae (*Marchantia*, *Lunularia*), and by their continuous growth the gemma cups (Figs. 381, 382) are always kept well filled.

One of the most interesting cases of adventitious budding is the formation of adventitious embryos in ovules ; in most instances this leads to POLYEMBRYONY, *i.e.* the presence of several embryos within the one seed. In addition to cases in which the additional embryos cannot be strictly regarded as adventitious but arise by fusion of ovules, by division of the nucellus within the integments, or by the existence of a number of embryo-sacs in one nucellus, normal ovules with only one embryo-sac may produce a number of embryos. In the latter case the embryo-sac may in rare instances (*Santalum*, *Sinningia*) contain two egg-cells, or a dichotomy of the embryo or its suspensor may occur. As a rule the condition is due to adjoining vegetative cells growing into the embryo-sac and there developing like sexually produced embryos. These adventitious embryos, which were first discovered by Strasburger, usually originate from cells of the nucellus (*Funkia ovata* (Fig. 240), *Euonymus latifolia*, *Citrus aurantium*, *Nothoscordon fragrans*, *Mangifera indica*, *Coelebogyne illicifolia*, *Clusia alba*, *Opuntia vulgare*, *Euphorbia dulcis*, *Colchicum autumnale*) more rarely from the inner integuments (*Allium odorum*). In many other plants (*Gnetum*, *Ulmus*) embryos may develop from the synergidæ or the antipodal cells. At the same time the egg-cell previously existing in the embryo-sac is able to continue its development after fertilisation, but is usually prevented from so doing by the adventitious embryos. The seeds in such cases would no longer contain the products of sexual reproduction, but

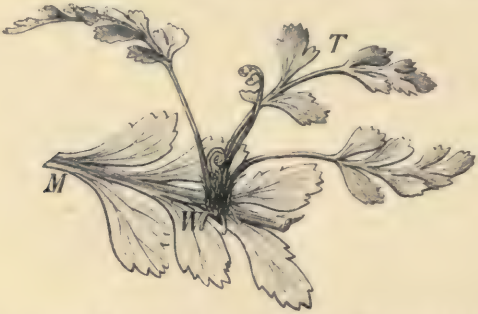


FIG. 239.—*Asplenium Fabianum*. A young plant (*T*), with leaves and roots (*W*), has sprung from the leaf (*M*) of the older plant.

would be degraded to organs of vegetative multiplication. The adventitious germs in the polyembryonic seed are, however, so far dependent upon sexual reproduction, that for the most part they only attain their development in case pollination has previously taken place; but in *Coelebogyne*, one of the Australian Euphorbiaceae, of which usually only female specimens are found in cultivation, and in *Balanophora elongata* and *Elatostema acuminatum* according to TREUB, and *Bal. globosa* according to LOTSY, the adventitious germs develop without the stimulus of fertilisation. These plants accordingly afford examples of APOGAMY, or of the substitution of a vegetative for a sexual mode of reproduction, such as occurs in certain ferns.

In the apogamous ferns vegetatively produced plants arise on the prothallus in the position of the sexual organs. This is found in different degrees in *Athyrium filix femina*, var. *cristata*, *Aspidium falcatum*, *Todea africana*, *Pteris cretica*, and in *Nephrodium pseudo-mas.* var. *polydactyla*. In the latter examples the sexual organs are no longer formed, although the young plants arise, by a vegetative process of budding, from exactly the same part of the prothallium where the archegonia would have been developed. FARMER, MOORE, and DIGBY have shown that in *Nephrodium* the origin of the apogamous bud is preceded by fusion of nuclei of vegetative cells of the prothallus. In the case of *Aspidium filix mas.* var. *cristatum*, etc., the apogamy seems to have resulted from cultivation. In a broad sense the development of bulbils in the place of flowers, in the species of *Allium*, might be considered as an example of apogamy (106).

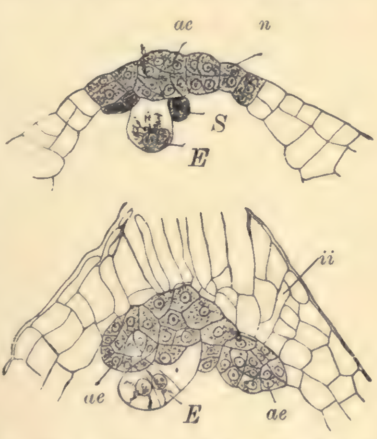


FIG. 240.—Vegetative formation of embryos in *Funkia ovata* (*Hosta coerulea*) by the budding of the nucleus; *n*, nucellus with cells in process of forming the rudiments (*ae*) of the adventitious embryos; *S*, synergidæ; *E*, egg-cell, in the lower figure developing into a sexually-produced embryo; *ii*, inner integument.

The cases of parthenogenesis described in recent years among the higher plants (Compositae, *Alchemilla*, *Thalictrum*, *Bryonia* ?) may be regarded as examples of a further peculiar type of apogamy. The ovum develops into an embryo without fertilisation, but since the reduction division has been omitted from the processes leading to its differentiation the egg cell has in these cases lost the characteristics of a female sexual cell and corresponds to a purely vegetative cell. The same will probably be found to be the case in *Wikstroemia indica*, *Ficus hirta*, and *Chara crinita* which are also parthenogenetic (107).

In some cryptogamic plants (*Marsilia*, *Saprolegnia*) as among lower animals, true parthenogenesis occurs. LOEB found that solutions which withdrew water ($MgCl_2$, other salts, sugar, urea) could stimulate the ovum to parthenogenetic development. WINKLER used extractives derived from the sperm, while NATHANSOHN showed that sometimes a rise of temperature could interrupt the resting state of an ovum awaiting fertilisation and lead to a parthenogenetic development. Jickeli regards the common feature of the various causes which lead to parthenogenesis to be that they are injurious influences, the effect of which, however, must not be carried too far ([108]).

Vegetative Multiplication by Single Cells (Spores).—As in the case of multicellular vegetative bodies, multiplication can be effected also through the separation of single cells. Strictly speaking, this manner of multiplication actually takes place whenever a division of the vegetative body occurs in unicellular Bacteria, Fungi, and Algae. Cells which serve the purpose of vegetative reproduction, and have a special form and method of development (spores, conidia, swarm-spores, gemmae), are first met with in the higher Cryptogams. They are frequently formed in special organs or receptacles (sporangia, conidiophores, fruit bodies).

As a Fern-plant occasionally arises directly from the tissue of the prothallus without the intervention of the sexual act, so also spore formation is occasionally omitted, and the prothallus arises vegetatively from the leaf of the sporophyte (apospory in varieties of *Athyrium*, *Aspidium*, *Asplenium dimorphum*, *Nephrodium pseudo-mas.* var. *cristata apospora*) ([108a]).

Sexual Reproduction

For the purpose of sexual reproduction two kinds of cells, male and female, are produced. Although neither alone is as a rule capable of development, the actual reproductive body is formed by the fusion into one cell of two such sexually differentiated cells. The elements of the male and female nuclei remain for a longer or shorter time distinguishable in the nucleus resulting from their fusion ([109]).

In fertilisation, as a rule, two uninucleate cells fuse, even when the vegetative protoplasts are multinucleate. In *Albugo Bliti*, *A. portulacae* and *A. tragopogonis*, however, Stevens found that the numerous nuclei of the ovum fused with an equal number of sperm nuclei. Probably other cases of this kind may be found.

The further development of non-nucleated fragments of the egg when united with a spermatozoid has been shown to occur among animals by O. and R. Hertwig, Boveri, and Delage. This phenomenon which is termed merogony has also been observed by Winkler in *Cystoseira barbata*, one of the Fucaceae ([110]).

In connection with parthenogenesis it was noted above that the incapability of further development which characterises the unfertilised ovum may be overcome by other means than copulation with the male cell; Klebs had already shown this to be the case with the gametes of certain Algae. It is thus necessary to distinguish in fertilisation between a stimulus, which removes the arrest laid on the further development of the ovum, and the cell fusion, which influences the nature of the resulting organism (amphimixis). The two influences are united in the case of natural fertilisation ([111]).

As it is thus necessary in sexual reproduction not only to provide for the production of male and female cells, but also to ensure their union, it becomes at once evident that, for sexual reproduction, the organs must have a different structure than if they were designed solely for vegetative activity. The sexual organs accordingly often exhibit a special and peculiar form, and differ materially in appearance from the vegetative parts of a plant.

The Union of Sexual Cells (Fertilisation).—Leaving out of consideration the necessary contributory external contrivances, fertilisation is accomplished by means of a chemotactic or chemotropic stimulus (pp. 266, 286). It is generally the non-motile egg-cells or the female sexual organ which exert an attractive influence upon the motile male cells. When, however, there is no difference in the external form of the male and female cells, then both are usually motile, and the attraction seems to be exerted mutually. This is probably the case with the motile and externally similar sexual cells (GAMETES) of the lower Cryptogams, particularly of the Algae (Fig. 97). In the conjugation of the Conjugatae, however, although both sexual cells are externally alike, one cell alone is usually motile, and passes through the connecting canal to the other. The capacity of the male cells for independent movement is common to most Algae, with the exception of the Florideae, in which the non-ciliated male cells are passively conveyed to the female organ by the water. Throughout the whole group of the higher Cryptogams, and in a few Gymnosperms, the male cells are motile spermatozoids, capable of seeking out the non-motile egg-cells concealed within the archegonia. But in the sexually differentiated Fungi the male substance usually remains enclosed in special hyphae which press themselves close against the female organs, and, by the perforation of the intervening cell wall, the fusion of their contents is rendered possible. The fertilisation of the Phanerogams is accompanied by a perforation of the intervening cell walls similar to that which occurs in the Fungi. In this case the male cell is enclosed within the microspore (pollen grain); the female, as a naked egg-cell, is included in the megaspore (embryo-sac), which in turn lies in the ovule, and in the Angiosperms the ovule is again enclosed within the ovary. The double-walled pollen grains possess no independent power of movement, but are conveyed to the female sexual organs by the assistance of external agencies (animals, currents of air or water). The pollen grain then grows out into a tube which is acted upon by chemotropic (including hydrotropic and aerotropic) influences, and grows like a fungal filament through the tissues of the ovary and ovule until it penetrates to the egg-cell in the embryo-sac; the union of the sexual cells is then easily effected (Fig. 99).

Recent researches have shown that in addition to the fusion of the generative cell with the ovum the second generative cell frequently fuses with the nucleus of the embryo-sac. This has been termed DOUBLE-FERTILISATION. The endosperm, which arises from the resulting nucleus, is thus, like the embryo itself, a product of fusion. This explains the hybrid character of the endosperm in the phenomenon of XENIA. In these cases characters of the pollen-parent appear in the ripening seed and not, as is usual, only in the descendants of the union. This is especially well shown in the maize when, *e.g.* blue- and yellow-fruited races or a race the fruits of which contain sugar and one in which they contain starch are interbred. It is uncertain what significance is to be attached to this so-called double fertilisation;

possibly the explanation is that the embryo-sac nucleus, as a sister nucleus to that of the ovum, exercises a similar chemotactic influence, and thus attracts the male generative cell, the fusion being of secondary importance since the endosperm is destined to be used as food by the embryo (112).

While one healthy pollen grain should be able to fertilise one healthy ovule, experience shows that better results follow from more liberal pollination of the stigma. This depends, according to CORRENS, on the fact that not every pollen grain (and not every ovule) is good. Thus in *Mirabilis jalapa* for each fertile pollen grain four are found infertile, and for every three good ovules there is one bad one. For *Mirabilis longiflora* the corresponding ratios are 1 : 3 and 1 : 1 (113).

To render certain the accomplishment of this POLLINATION, or conveyance of the pollen to the female sexual organs, special and often complicated contrivances are made use of by the different Phanerogams, according to the means of conveyance upon which they are dependent.

Plants, the pollen of which is carried by wind, are designated ANEMOPHILOUS. As this method of conveyance depends upon the chance of wind direction, the production of an enormous amount of pollen characterises wind-fertilised plants. According to Holden a medium-sized plant of maize produces about 50,000,000 pollen grains.

Such enormous quantities of pollen are often taken up from pine forests by the wind that clouds of pollen fill the air. The surface of Lake Constance in spring is so thickly covered with pollen that it is coloured yellow ("the lake blooms," it is then said), and in the Norwegian fiords, at a depth of 200 fathoms, the pollen of Conifers, according to F. C. NOLL, forms for a time the principal nourishment of a Rhizopod (*Saccamina*).

The male flowers of such anemophilous plants are accordingly either freely exposed to the wind in Catkins (Coniferae, Querciflorae), or the versatile anthers, as in the Grasses, depend from long, lightly-swaying filaments. The pollen grains themselves do not stick together but escape from the opened anthers in the form of fine powder. The pollen grains of many Conifers are rendered extremely buoyant and easy of conveyance by the wind by two sac-like protrusions of the exine. In some anemophilous plants the pollen is discharged by the sudden extension of the filaments, previously rolled up in the bud (Urticaceae, *e.g. Pilea*), or by the hygroscopic tension of the anthers. The female organs are also often specially adapted for the attachment of the pollen thus floating in the air. The stigmas either spread out like a brush (*Corylus*), or are finely feathered or provided with hairs (Grasses, Walnut), or drawn out into long threads (Indian Corn). In the Conifers, with freely exposed ovules, the grains of pollen are caught and retained in a drop of fluid exuded from the micropyle, into which they are gradually drawn as the fluid dries up. In other Conifers whose ovules are concealed in the cone of the female inflorescence, processes of the integument catch the pollen and conduct it to the sticky opening of the young ovules.

For the fertilisation of the higher plants, the presence of water is not so essential as it is for most Cryptogams. Only a few submerged

Phanerogams make use of the agency of water for effecting their pollination, and are, on that account, termed HYDROPHILOUS PLANTS.

The pollen of the submerged *Zostera* exhibits certain peculiarities, distinctly referable to the necessity of effecting fertilisation under water. It does not form round grains, but in their place elongated thread-like filaments devoid of an exine, which, as they have the same specific weight as the surrounding water, are easily set in motion by the slightest currents, and are thus brought into contact with the stigmas. In the case of the submerged water plants, *Vallisneria*, *Elodea*, and species of *Enhalus*, found in the Indian Ocean, the pollination is accomplished on the surface of the water. Thus, for example, the male flowers of *Vallisneria*, after separating from the parent plant, rise to the surface of the water, where they open and float like little boats to the female flowers, which, by the elongation of their spirally coiled flower-stalks, ascend, at the same time, to the surface of the water, only to become again submerged after fertilisation ([114]).

In the great majority of Phanerogams pollination is effected by means of animals. By enticing in various ways insects, birds, bats, or snails, plants are enabled not only to utilise the transporting power but also the intelligence of animals in the service of pollen-conveyance. The pollination is then no longer left to chance; and as the transport of pollen to the sexual organs becomes more assured, the necessity for its formation in such enormous quantities as in anemophilous plants is obviated. For the most part, such plants are adapted to POLLINATION BY INSECTS (ENTOMOPHILY). For their nourishment, plants offer not only the sugary sap, which, as nectar, is excreted from different parts of the flowers, but also the pollen itself, which furnishes a nitrogenous food material and, together with the honey, is kneaded by bees into bee-bread. As additional means of enticement, and to attract animals from a distance to the nectar offered by the sexual organs, special perfumes and conspicuous colours have also been developed. The ATTRACTIVE APPARATUS of plants is generally formed by the coloured floral leaves; by the outer floral leaves or calyx (*Nigella*, *Aconitum*), or by the perianth (Lily, Tulip), or by flowers specially modified for this purpose (outer florets of the Compositae, Umbelliferae, and *Viburnum opulus*; scented flowers of *Renanthera Lowii*). Bracts and portions of the axis which do not belong strictly to the flower occasionally serve the same function as in the circumfloral attractive apparatus of the Euphorbiaceae or the extra-floral attractive apparatus of *Astrantia major*, *Salvia*, *Melampyrum*, *Dalechampia*, *Bougainvillea spectabilis*, and the Aroideae.

The pollen of the entomophilous, in contrast to that of the anemophilous plants, is not a dry powder, but its grains are stuck together with an oily or mucilaginous fluid; in other cases, they are held together by their rough outer surfaces or by means of viscid threads (*Oenothera*), and can only be removed from the anthers by animals. The structure of the flower is so contrived, as CHRISTIAN

CONRAD SPRENGEL first pointed out in 1793 in his famous work on the structure and fertilisation of flowers ("Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen"), that the pollen grains must necessarily become attached to certain parts of the body of the animal visiting it in search of food, and so be conveyed to the sticky or hairy stigma of other flowers. The variety of means employed to secure pollination, and the wonderful adaptation shown by the flowers to the form and habits of different insects, are most remarkable.

In addition to the stimulus of hunger, plants utilise the reproductive instinct of insects for securing their pollination. Not a few plants (*Stapelia*, *Aristolochia*, and members of the Araceae), by the unnatural colour of their flowers, combined with a strong carrion-like stench, induce carrion-flies to visit them and deposit their eggs; in so doing they effect, at the same time, the pollination of the flowers. In the well-known hollow, pear-shaped inflorescences of the Fig (*Ficus carica*, Fig. 575), there occur, in addition to long-styled female flowers that produce seeds, similar gall-flowers with short styles. In each of the latter a single egg is laid by the Gall-wasp (*Blastophaga*), which in effecting this pollinates the fertile flowers with pollen carried from the male inflorescence (the Caprificus). The large white flowers of *Yucca* (Fig. 493) are exclusively pollinated by the Yucca moth (*Pronuba*). The moth escapes from the pupa in the soil at the time of flowering of *Yucca* and introduces its eggs into the ovary by means of the style; in doing this it carries pollen to the stigma. The larvæ of the moth consume a proportion of the ovules in the ovary, but without the agency of the moth no seeds would be developed, as the sterility of the plant in cultivation shows.

In South America the humming-birds are especially active in the conveyance of pollen, as they seek for insects in the flowers; a starling visits the flowers of species of *Puya* to drink the watery nectar. In the Old World the honey-birds play a similar part. MARLOTH enumerates about forty ornithophilous plants from the South African flora; these are mostly pollinated by species of *Nectarinia*. Species of *Feijoa* have sweet succulent perianth leaves to attract the birds, which serve to convey the pollen.

Besides these ORNITHOPHILOUS plants there are a few visited by Bats (CHIROPTEROPHILOUS); thus the diœcious Pandanaceous plant *Freycinetia* is pollinated by a Flying Fox (*Pteropus*), which eats the inner bracts.

Pollination in some cases is effected by means of snails (MALACOPHILOUS PLANTS). To their instrumentality the flowers of *Calla palustris*, *Chrysosplenium*, and also the half-buried flowers of the well-known *Aspidistra* owe their pollination ([115]).

Self- and Cross-Fertilisation.—It has already been pointed out that it is by sexual reproduction, in contrast to the vegetative mode of multiplication, that qualitative modifications are effected. Such qualitative changes are best attained when the sexual cells are derived from different individuals. It is in accordance with this same principle that, in the sexual reproduction of plants, varied and often complicated contrivances are manifested, which conduce to CROSS-FERTILISATION (union between sexual cells of different individuals), even when the individuals themselves are HERMAPHRODITE and possess two kinds of sexual organs, as in the case of the majority of Phanerogams.

As, however, self-fertilisation takes place also in a number of plants, either regularly or as a makeshift, it is evident that whatever may be the advantage derived from a union of two distinct individuals, it is no more essential for sexual reproduction than for vegetative multiplication. Self-pollination, although regularly occurring, frequently fails to occasion self-fertilisation, as often the pollen will not develop pollen-tubes on the stigmas of the flower (self-sterile) by which it was produced, but only on those of different flowers (*Secale cereale*, *Corydalis cava* and some Cruciferae, *Lobelia fulgens*, *Verbascum nigrum*, etc.) ([116]).

The antipathy between the sexual organs of the same flower, in certain plants, so greatly exceeds the bounds of indifference that they act upon each other as poisons. Thus, for example, it is known of certain Orchids that pollination with their own pollen causes the death of the flower, while in other cases the pollen is killed in a short time by the stigmatic fluid of the same flower.

In other instances, self-fertilisation occurs where cross-pollination either is not effected, or else as an alternative to it (Wheat, Barley, *Canna*, *Viola* species, *Linum usitatissimum*, etc.). By many plants, in addition to the large "chasmogamous" flowers adapted to insect pollination, small, inconspicuous flowers are produced which, usually concealed underground or by the lower leaves, never open, and only bear seeds which have been produced by self-fertilisation. In such flowers the stamens no longer open, the pollen-tubes growing through the wall of the anther to reach the stigma. In some plants the majority of the seeds are derived from such CLEISTOGAMOUS flowers (*Viola*), and sometimes their seeds alone are fruitful (*Polycarpum tetraphyllum* possesses only cleistogamous flowers). As the greater number of such plants, however, in addition to the seeds of the self-fertilised small cleistogamous flowers, produce seeds resulting from the cross-fertilisation effected in the larger flowers (*Impatiens noli-tangere*, species of *Lamium*, *Specularia perfoliata*, *Stellaria*, *Juncus bufonius*, etc.), the ancestral plants of the cleistogamous generations, as well as their descendants, have, at least, the opportunity for cross-fertilisation open to them.

Special contrivances for ensuring the crossing of the sexual cells, particularly by preventing self-pollination, are found to exist throughout the whole vegetable kingdom.

Self-pollination is most effectually avoided when the plants are unisexual, that is when there are both male and female plants. Such DIŒCIOUS plants exist in almost all classes of plants from the lower Cryptogams to the most highly developed Phanerogams (certain Mucorineae, many of the lower Algae, species of *Fucus*, *Marchantia*, *Polytrichum*, Equisetaceae, *Taxus*, Hemp, Hops, Date-Palm, etc.) In

MONŒCIOUS plants (other Mucorineae, Algae, species of *Carex*, *Ricinus*, Box, Coniferae, Cupuliferae, etc.) the male and female organs occur on different flowers, but the flowers are borne on the same plants. The fertilisation between different flowers is thus secured; but even here crossing with other individuals is, for the most part, assured by dichogamy.

The term DICHOGAMY is used to denote the fact that the male and female sexual organs attain their maturity at different times. When either the male or female sexual organ matures before the other, the self-pollination of morphologically hermaphrodite flowers is avoided and crossing ensured. Both hermaphrodism and monœcism are more advantageous than diœcism, as all the individual plants in such cases are able to produce seeds; while in diœcious plants the male flowers cannot be utilised for the direct production of seeds. Dichogamy secures crossing in such a simple manner, and is so easily attained by hermaphrodite plants, that it is of very general occurrence in the vegetable kingdom. According to the priority of the maturity of their sexual organs, plants are designated PROTANDROUS or PROTOGYNOUS.

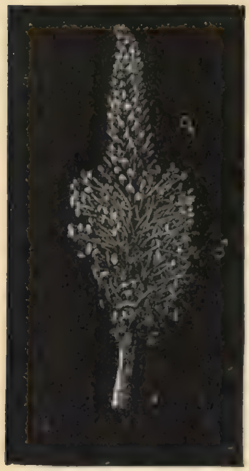


FIG. 241.—Inflorescence of *Plantago media* with protogynous flowers. The upper, still closed flowers (♀) have protruding styles; the lower (♂) have lost their styles, and disclose their elongated stamens.

PROTANDRY, the earlier maturing of the male sexual organs, is the more frequent form of dichogamy. It occurs in the flowers of the Geraniaceae, Campanulaceae, Compositae, Lobeliaceae, Umbelliferae, Malvaceae, etc. The anthers, in this case, open and discharge their pollen at a time when the stigmas of the same flowers are still imperfectly developed and not ready for pollination. Accordingly, PROTANDROUS FLOWERS CAN ONLY BE FERTILISED BY THE POLLEN OF YOUNGER FLOWERS.

In the less frequent PROTOGYNY the female sexual organs are ready for fertilisation before the pollen of the same flowers is ripe, and the stigma is usually pollinated and withered before the pollen is shed; so that the PROTOGYNOUS FLOWERS MUST BE FERTILISED BY THE POLLEN OF OLDER FLOWERS (*Anthoxanthum odoratum*, *Luzula pilosa*, *Scrophularia nodosa*, *Aristolochia clematitis*, *Helleborus*, *Magnolia*, *Plantago*, Fig. 241).

A still more complicated method of effecting cross-fertilisation, because involving also morphological and anatomical differences of structure, results from HETEROSTYLY, or the peculiarity of some species of plants of producing stigmas and anthers which vary in height in different individuals of the same species. In contrast to the unlimited possibility of crossing in other hermaphrodite flowers (panmixia), there is here a limitation to certain classes of individuals of the species. A good example of heterostyled flowers is afforded by the Chinese Primrose (Fig. 242). This plant has two forms of flowers, long-styled (*L*) and short-styled (*K*), while the positions of the stigmas and anthers in the two kinds of flowers are exactly reversed. The pollen grains of the short-styled flowers, moreover, are larger, and the stigmatic papillæ shorter, than in those with the longer styles (*p*, *P*, and *n*, *N*). The purpose of such morphological and anatomical differences existing between flowers of the same species was first understood after they were discovered by DARWIN to be a contrivance for cross-pollination. Fertilisation is most successful in such cases when the pollination of the stigmas is effected by the pollen of anthers correspondingly situated. By such a "legitimate" fertilisation, more and better seeds are produced than by "illegitimate" fertilisation, and in some cases (*Linum perenne*, *Fagopyrum esculentum*) legitimate fertilisation alone is productive. Legitimate fertilisation is rendered more certain by the fact that insects in visiting the flowers touch correspondingly placed sexual organs with the same portions of their body. The flowers of Primroses have styles of two different lengths (DIMORPHIC HETEROSTYLY); the same peculiarity is exhibited by *Pulmonaria*, *Hottonia*, *Fagopyrum*, *Linum*. There are also flowers with TRIMORPHIC HETEROSTYLY (*Lythrum Salicaria*, and some species of *Oxalis*), in which there are two circles of stamens and three variations in the height of the stigmas and anthers.

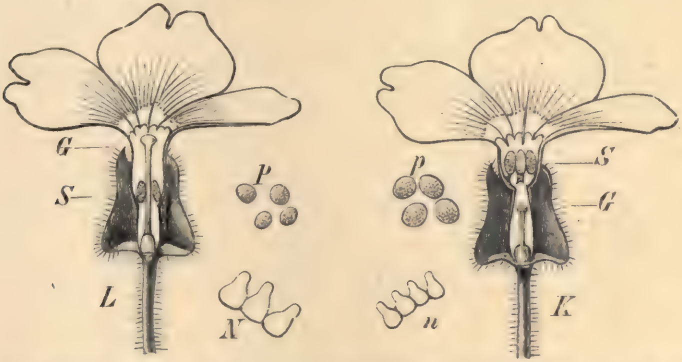


FIG. 242.—*Primula sinensis*: two heterostyled flowers from different plants. *L*, Long-styled; *K*, short-styled flowers; *G*, style; *S*, anthers; *P*, pollen-grains, and *N*, stigmatic papillæ of the long-styled form; *p* and *n*, pollen-grains and stigmatic papillæ of the short-styled form. (*P*, *N*, *p*, *n*, × 110.)

The different forms of heterostylic plants do not only differ in the length of the style and stamens, and in the colour and size of the pollen grains, but according to ERRERA commonly exhibit differences in form of leaf, in the size and colouring of the flowers, and in the weight of the seeds.

In a great number of flowers self-pollination is made mechanically impossible, as their own pollen is prevented by the respective positions of the sexual organs from coming in contact with the stigma (HERCOGAMY). In the Iris, for example, the anthers are sheltered under the branched petaloid style, upon whose lip-like stigma no pollen can come, unless through the agency of insects, and in the protogynous flower of *Aristolochia clematitis* pollination from the anthers, which occupy a lower position on the column, is prevented. The conveyance of pollen from the older to the younger flowers is effected in *Aristolochia* by small insects. The flowers at first stand upright with a widely opened mouth (Fig. 243 *I*) and in this condition the insects can easily push past the downwardly directed hairs clothing the tubular portion of the corolla and reach the dilated portion below. Their exit is, however, prevented by the hairs until the stigma has withered and the anthers have shed their pollen. When this has taken place (Fig. 243 *II*) the hairs dry up and the insects covered with pollen can make their way out and

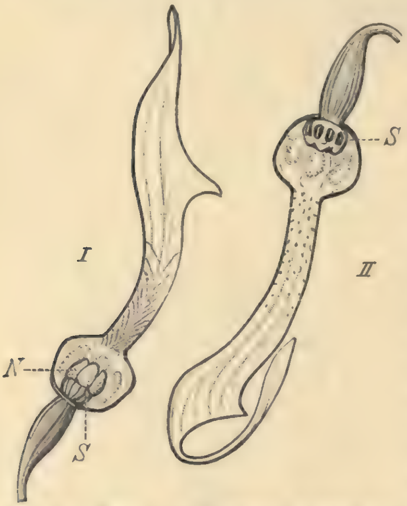


Fig. 243.—Flowers of *Aristolochia clematitis* cut through longitudinally. *I*, Young flower in which the stigma (*N*) is receptive and the stamens (*S*) have not yet opened; *II*, Older flower with the stamens opened, the stigma withered, and the hairs on the corolla dried up. (× 2.)

convey the pollen to the receptive stigmas of younger flowers. In the Orchidaceae and Asclepiadaceae self-pollination is rendered impossible both by the nature of the pollen masses and by their position. A complicated form of structural contrivance, by means of which cross-pollination is secured, may be seen in a flower of *Salvia pratensis* (Fig. 244). The anthers of this flower are concealed in the upper lip of the corolla, from which the style, with its bilobed stigma, projects. When a bumble-bee visits the flower in search of honey, it must first with its proboscis push out of the way the small plate (*s*), formed of two sterile anther halves grown together. These are situated at the ends of the short arms of the connectives (*c*), which are so elongated that they might easily be mistaken for the filaments (*f*) of the stamens. The fertile anther halves are situated at the other ends of the connectives, and are thus brought in contact with the hairy back of the bumble-bee when it pushes against the plate at the short ends of the lever-like connectives. The pollen thus attached to the bee will be brushed off its back by the forked stigma borne on the elongated style of an older flower (Fig. 244 *II*). Good examples of hercogamous flowers are afforded by the Papilonaceae, by *Kalmia*, whose anthers are held in pockets of the corolla and are only released when touched by a visiting insect (Fig. 245), by *Vinca*, etc.

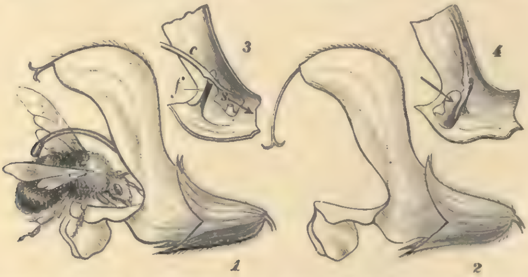


Fig. 244.—Pollination of *Salvia pratensis*. 1, flower visited by a bumble-bee, showing the projection of the curved connective from the helmet-shaped upper lip, and the deposition of the pollen on the back of the bumble-bee; 2, older flower, with connective drawn back, and elongated style; 4, the staminal apparatus at rest, with connective enclosed within the upper lip; 3, the same, when disturbed by the entrance of the proboscis of the bee in the direction of the arrow; *f*, filament; *c*, connective; *s*, the obstructing half of the anther.

Some plants bear in addition to hermaphrodite flowers others that are purely female. They are termed polygamous, and the distinction is made between gynodiœcious and gynomonœcious forms. In the latter the female flowers are borne on the same individual as the hermaphrodite flowers (*Aesculus*, etc.); in the former they are on distinct individuals (*Silene inflata*, *Erodium cicutarium*, *Satureja*).

Hybridisation.— The union of two sexual cells is, as a rule, only possible when they are derived from individuals of the same species; it is only then that they exercise an attractive influence upon each other and fuse together in the act of sexual reproduction. The sexual cells of Mosses and Ferns, apart from all other considerations, would not unite because the spermatozoids of Mosses are attracted to the female organs by sugar, while those of the Ferns are stimulated by malic acid. In the case of Phanerogams, a mixed union of sexual cells is likewise prevented by various obstacles to pollination and fertilisation. Occasionally, however, the sexual cells of different varieties, species, or even genera have shown themselves able to unite and produce descendants capable of development. Such a union is termed HYBRIDISATION, or bastard-formation, and its products HYBRIDS or BASTARDS.

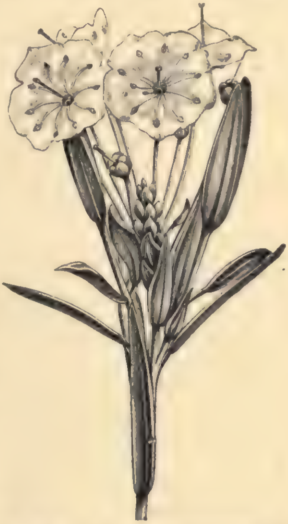


FIG. 245. — A small inflorescence of *Kalmia glauca*; the stamens are retained in pocket-like depressions of the corolla.

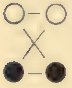
Through the demonstration of the possibility of hybridisation, the sexuality of plants, for a long time doubted, was indisputably proven. With this object in view, and following the work of FAIRCHILD, in 1717, hybrids were raised in great numbers by KÖLREUTER as early as 1761 (117). It also demonstrated that the real purpose of sexual union was the combination of the properties of both parents, for transitional forms are found among hybrids which in many characteristics resemble the male and in others the female ancestor (heterodynamic hybrids), or they may show an equal combination of the characters of both (homodynamic hybrids, *e.g. Nicotiana rustica* ♀ × *Nic. paniculata* ♂). Less frequently it happens that the hybrid resembles one ancestor almost exclusively. In such a case the attributes of the other ancestor remain latent, and may appear regularly or quite unexpectedly, through atavism (p. 299), in later generations.

The mingling of characters is often complete. Had one species simple leaves and the other compound, their hybrid would have leaves more or less cleft; or were the flowers of one parent species red and those of the other yellow, the hybrid frequently bore flowers with red and yellow markings (mosaic hybrids), or which were orange-coloured. If an early blooming form were crossed with a late bloomer, the hybrid would flower at a time intermediate between the two.

A large number of spontaneous hybrids have been found which have arisen naturally from plants with a special tendency to hybridisation. That such natural hybrids do not oftener occur is due to the lack of an opportune time or space for their development, and also to the fact that in the case of pollination of flowers with different kinds of pollen, that of their own species seems as a rule more effectual in effecting fertilisation (118).

The investigations of DE VRIES, CORRENS, TSCHERMAK, and others, have greatly increased our knowledge of the laws governing the inheritance of different characters of plants. No final conclusions are yet attained, however, since even in regard to limited portions of the problem new features are still becoming apparent (119).

In the crossing of closely related forms (varieties or nearly related species), Mendel's laws (called after their first discoverer, GREGOR JOH. MENDEL [1866] are found to hold. These laws, the most generally applicable of which is that of the segregration of characters, were independently rediscovered by DE VRIES and CORRENS. An example will give the best idea of these laws. If a red-flowered *Mirabilis jalapa* be crossed with a white-flowered individual one obtains a generation of hybrids with uniformly rose-coloured flowers. If these are fertilised from one another a second generation is obtained, but the individuals of this are not uniformly coloured; in addition to rose-coloured plants pure red-flowered and white-flowered plants occur in the proportion per cent of 50 : 25 : 25 *i.e.* in the ratio 2 : 1 : 1. When fertilised from one another the pure red-flowered plants produce a red-flowered progeny and the white-flowered plants also breed true; they have returned to the pure parent forms. The 50% of rose-coloured plants again splits in the next generation, and like the former generation yields 25% pure red, 25% pure white, and 50% rose-coloured plants. The proportion of hybrid plants thus continually becomes lessened by the return to the red and white types; in the eighth generation only 0·75% of hybrids remain, and this small remainder continues to split further on breeding. These results are theoretically explained by assuming that the sexual cells of the rose-flowered hybrids are not themselves of hybrid nature, but are already segregated into pure red and pure white sexual elements. In the process of fertilisation the union producing a hybrid, red × white (white × red, red × white) will occur twice as frequently as the union red × red or white × white which give rise to pure forms. This is illustrated in the accompanying diagram in which the dark circles represent the red sexual elements.



The characters in which the parents differ do not, however, always blend so that the hybrid exhibits an intermediate character. More usually the hybrids completely resemble in this respect either the paternal or maternal parent, the character of the one parent being dominant in the hybrid while the other remains latent (Law of dominant characters). This is the case for example in hybrids between *Urtica pilulifera* with serrate leaves and *U. Dodarti* (Fig. 246). The hybrids have all serrate leaves like *U. pilulifera*, so that in the second generation the proportion of serrate-leaved to entire-leaved individuals is per cent 75 : 25 (3 : 1). Only 50% of the serrate-leaved individuals are, however, of hybrid nature and continue to show a similar splitting of characters in the next generation; 25% have become pure *U. pilulifera*. It is impossible to predict which characters will prevail in any cross, and the question can only be settled by experiment; usually the phylogenetically younger character appears to be dominant.

When the parents differ in two characters instead of only one, instead of monohybrids, dihybrids result. It then appears that the several characters are independently transmitted and distributed in the descendants. Thus new combinations of characters may come about, a fact of great importance in plant-breeding. From the crossing of peas with yellow, wrinkled seeds and those with green, smooth seeds, among other possible combinations of the characters the new ones yellow-smooth and green-wrinkled appear (autonomy of characters). For two pairs of characters the ratio is 9 : 3 : 3 : 1, only four externally distinguishable combinations resulting, though the nine individuals are really different, the difference being masked in part by the dominance of certain characters. If *m* is the number

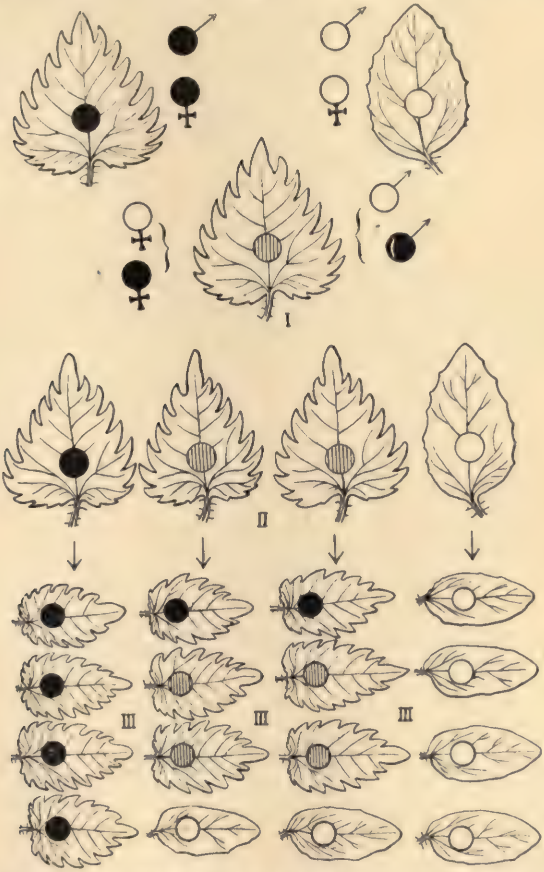


FIG. 246.—Hybridisation of *Urtica pilulifera* (to the left, above) with *U. Dodarti* (to the right). I, First generation which, though hybrid, shows the dominant leaf-form of *U. pilulifera*. Its sexual cells, in which a separation of the character occurs, give rise in generation II to a pure and constant *pilulifera*, a pure *Dodarti* and two hybrids. In generation III the pure forms to the right and left are constant, the hybrids in the centre show further splitting of characters.

of pairs of characters, the number of internally distinct combinations is 3^m, and the number of constant forms 2^m. If there are four pairs of characters there thus result 81 hybrid-combinations, and among these 16 constant forms.

Many characters, however, tend to remain associated together (coupled characters).

In crossing many races quite new characters frequently appear in the hybrids. Thus in crossing a white-flowered with a yellow-flowered *Mirabilis* there may result, besides white-flowered and yellow-flowered descendants, others with rose-, red-, red-white, yellow-white, rose-red, and rose-white coloured or striped flowers. Since these newly appearing characters each in turn obey the Mendelian laws it is assumed that they were latent in the parents, and that the latter belonged to what are called crpytomerous races.

The Mendelian laws hold also in the animal kingdom and for the human race, but only for the crossing of nearly related forms. Thus crosses between negroes and negro-albinos follow Mendelian laws, while those between negroes and whites do not.

The more closely allied the parent plants, the more readily, as a rule, may hybrids between them be produced. Many families seem to incline naturally to hybridisation (Solanaceae, Caryophyllaceae, Iridaceae, etc.); others again develop hybrids only occasionally or not at all (Papilionaceae, Convolvulaceae, Coniferae, etc.). Even in the same family the related genera and species exhibit great differences in the readiness with which they may be crossed. The Grape-vine, and also the Willow are easily crossed with other species of their own genus, and the same is also true of the different species of *Dianthus*, while the species of *Silene* cross with each other only with difficulty. Species hybrids are easily produced from species of *Nicotiana*, of *Verbascum*, and of *Geum*; on the other hand, it is very difficult to cross different species of *Solanum*, *Linaria*, or *Potentilla*. The hybridisation, however, of nearly allied forms is often impossible—the Apple with the Pear, for instance—although the Peach and Almond may be crossed, and also the species of even the different genera *Lychnis* and *Silene*, *Rhododendron* and *Azalea*, *Aegilops* and *Triticum*, *Secale* and *Triticum* (RIMPAU), *Zea* and *Euchlaena* (*Zea canina* results from a cross between *Z. mais* ♂ and *Euchlaena mexicana* ♀), each according to their "sexual affinity."

DERIVATIVE HYBRIDS arise when hybrids are crossed with one another, or with one of the original parent forms. In this way it has been possible to unite six species of Willow in one hybrid, and in the case of the Grape-vine even more species have been combined. It is only in rare cases, however, that the form of the hybrid remains constant in the succeeding generations. These exhibit more frequently a tendency to revert to one of the original ancestral forms.

In addition to their inherited qualities HYBRIDS EXHIBIT NEW PECULIARITIES not derived from their parent forms. These are a MODIFIED FERTILITY, GREAT TENDENCY TO VARIATION, and often a MORE LUXURIANT GROWTH. The fertility is often so enfeebled that the hybrids either do not flower (*Rhododendron*, *Epilobium*), or are sterile and do not reproduce themselves sexually. This enfeeblement of the sexuality increases the more remote is the relationship of the ancestral forms. Other hybrids such as those of *Salix* and *Hieracium* remain fertile.

The tendency to variability is often greatly enhanced in hybrids,

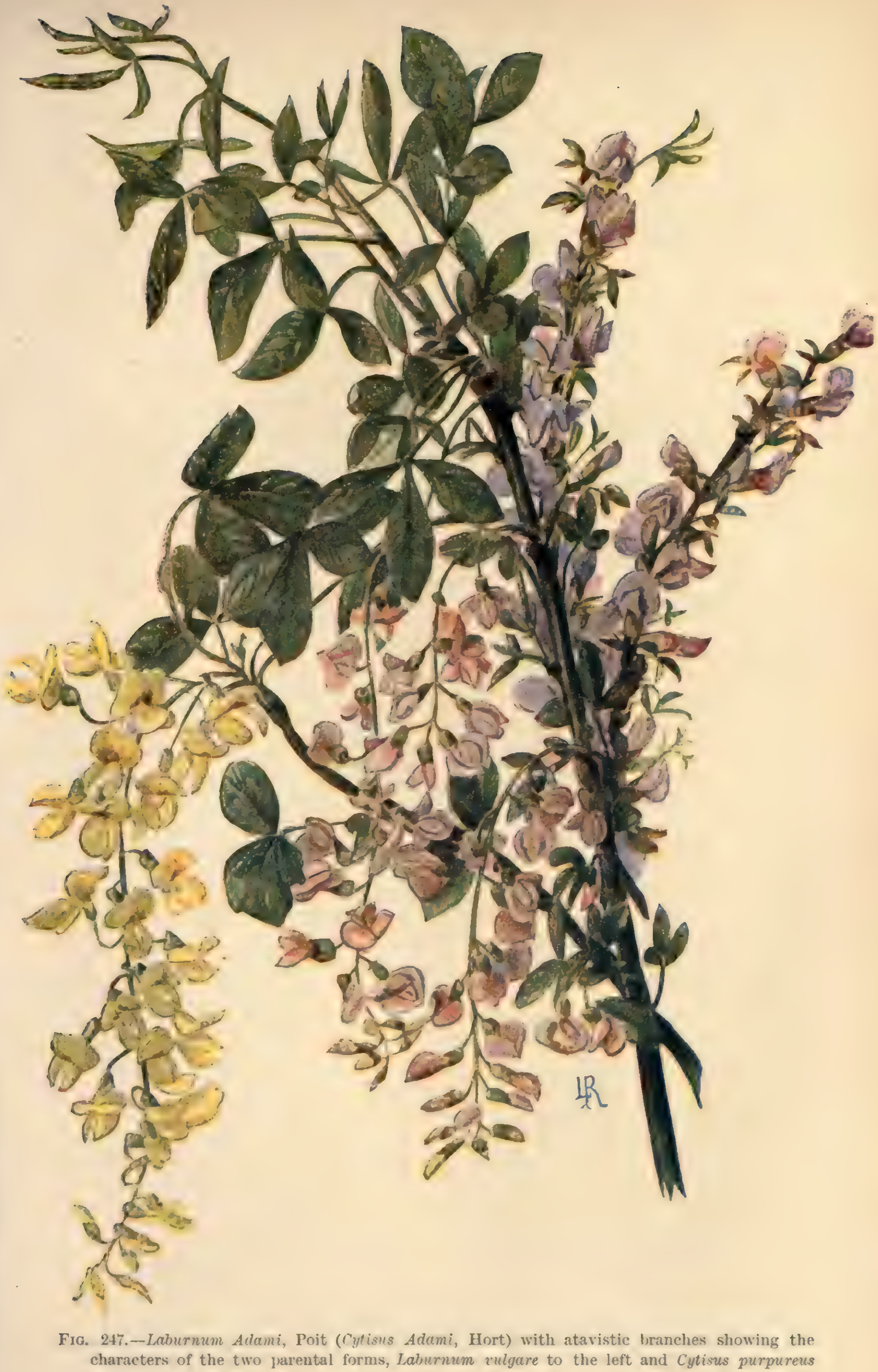


FIG. 247.—*Laburnum Adami*, Poit (*Cytisus Adami*, Hort) with atavistic branches showing the characters of the two parental forms, *Laburnum vulgare* to the left and *Cytisus purpureus* to the right.

especially in those arising from the hybridisation of different varieties of the same species.

Hybrids, particularly those from nearly related parents, frequently produce more vigorous vegetative organs, they bloom earlier, longer, and more profusely than the uncrossed plants, while at the same time the flowers are larger, more brilliant, and exhibit a tendency to become double. The luxuriance of growth and the increased tendency to produce varieties displayed by the hybrids have made the whole subject of hybridisation one of great practical as well as theoretical importance.

It is doubtful if hybrid forms can be produced (graft-hybrids) by a vegetative union of portions of two different plants (grafting, budding); *Laburnum Adami* (Fig. 247), and more recently an intermediate form between *Mespilus germanica* and *Crataegus monogyna* ([120]), appear to be of this nature. As yet, however, attempts to experimentally obtain these forms by vegetative or sexual methods have not succeeded. (Cf. p. 252.)

The Dissemination and Germination of Seeds

If the seeds after their separation from the parent plant simply fell upon the earth, the young seedlings would be injuriously restricted to the place already occupied by the parent plant, and would also spring up in such large numbers that they would mutually exterminate each other. The dissemination of the seeds thus becomes a necessity, and although a larger or smaller proportion perish in the process, a small number eventually find themselves in a favourable environment.

For their DISSEMINATION, seeds (and also spores and other reproductive bodies) make use of the same agencies as are employed for the conveyance of pollen. Thus their dispersion is effected by means of currents of air and water, by their forcible discharge from their receptacles and by animals; to these means must now be added human intercourse as a by no means unimportant mode of dispersal.

To ensure the dispersal of seeds by the wind, all those contrivances are of use which serve to increase their superficial area with but small augmentation of their weight. Of this nature are the hairy appendages of seeds and fruits, as in *Gossypium*, *Epilobium*, *Populus*, *Salix*, *Typha*, *Clematis*, and the fruits of the Compositae with their pappus, of *Valeriana*, etc. Compared with the accelerated fall in a vacuum, the retardation exerted by the resistance of the air (by which the opportunity for dispersal through the agency of the wind is enhanced) in the case of *Cynaria Scolymus* is, in the first second, as six to one. Similar adaptations for utilising the agency of the wind as a means of dispersal are the wing-like appendages formed from the expansion of the sepals (*Dipterocarpus*) or of the ovary (*Acer*, *Fraxinus*, *Ulmus*, *Polygonum*, *Robinia*, *Gleditschia*, and the fruits of many Umbelliferae), or of the seeds themselves, as in the winged seeds of the

Bignoniaceae and many Ternstroemiaceae). In a seed of one of the Bignoniaceae (Fig. 248), with its widely outspread, glossy wings, the centre of gravity is so disposed that the seed floats lightly along through the air in an almost horizontal course, and with a motion like that of a butterfly. The seeds of *Zanonia*, one of the Cucurbitaceae, are very similarly equipped. In the Lime the subtending leaf which is attached to the inflorescence is retained to facilitate the dispersal of the fruits by the wind; and in the seeds of the Fir the winged appendages are derived from the tissue of the placental scale. The aerial transportation of seeds and fruits, winged only on one side, is accompanied by a continuous spirally twisting movement which assists to retard their fall. Thus in the above-mentioned *Bignonia* DINGLER found the retardation in the first second amounted to thirty times the free fall, and in *Pinus silvestris* to seven times.

The diminutive size of many reproductive bodies, and the proportionate enlargement of their surface in comparison with their volume, increase their buoyancy. Microscopically small Fungi, spores, and Bacteria are in consequence easily transported by the wind. According to FALCK's observations even the heat produced by the respiration of a fructification of a fungus is sufficient to suspend the spores in the air. In the spores of *Lycoperdon caelatum* DINGLER found the retardation to be as 1 to 1000, which, according to NAGELI, could only be theoretically explained by the supposition that the retardation was intensified by a thin layer of air permanently adhering to the surface of the spores (121).

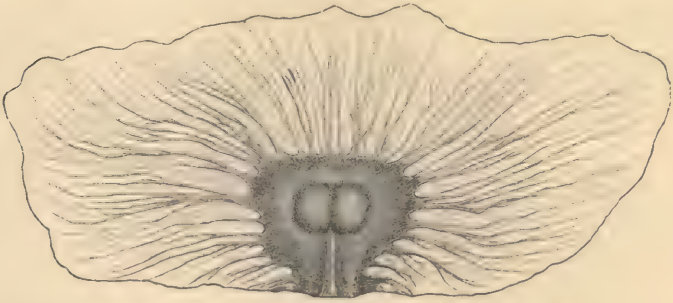


FIG. 248.—Winged seed of *Pithecoctenium echinatum*. (Nat. size.)

Minute dust-like spores and seeds form the most effective means of dispersal, as was shown in the return of vegetation to the island of Krakatoa, where the flora was destroyed by a volcanic eruption in 1883. Following the forms with minute seeds or spores came those with hairy fruits or seeds, and later than these the winged seeds.

Seeds and fruit are also frequently transported great distances by the agency of WATER. In the case of maritime plants the seeds are often especially adapted (water-tight floating tissues (Fig. 249); large air-spaces serving as swimming-bladders, etc.) for transport by ocean currents. Through the possession of such devices, the seeds of West Indian plants are carried to Norway by the Gulf Stream, as was known to LINNÆUS, and the appearance of Coco-nut palms as the first vegetation on isolated coral islands is in like manner due to the adaptation of their fruits to transport by water. SCHIMPER was able to show in detail the value of ocean-currents for the geographical distribution of the strand-flora (122).

ANIMALS participate largely in the dissemination of seeds; either by eating the agreeably tasting and often attractively coloured fruit, and excreting the undigested seeds, or by their involuntary transportation of seeds and fruits which have become in some way attached to them. This is effected in many cases by hooks and bristles (*Lappa*, *Galium aparine*, *Bidens*, *Echinospermum*, *Xanthium*, and the fruits of *Medicago minima*, so common in sheep's wool and erroneously termed wool-lice). The seeds may also become attached to animals by means of some sticky substance ; in this way the seeds of the Mistletoe, which stick to the beaks of birds eating the berries, finally adhere to the branches of trees upon which the birds wipe their bills. The widespread distribution of fresh-water plants can only be accounted for through the agency of aquatic birds.

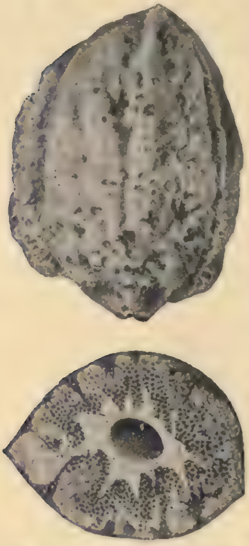


FIG. 249.—Fruit of *Terminalia catappa* from the drift. In the upper specimen the corky floating tissue is seen from the outside, the smooth, superficial layer being already worn away. The lower figure is of a cross section through the floating tissue ; the seed has been removed. (After SCHIMPER.)

The natural distribution of plants has been greatly modified by the interference of man, especially in these days of universal commercial intercourse by rail and sea. By their instrumentality not only have the useful plants been widely distributed over the earth, but the weeds have followed in the same way ; and many a seed thus accidentally carried to other lands has finally found there a new place of growth.

The forcible discharge of spores and seeds is effected by the sudden liberation of hygroscopic or tissue tensions. It has already been mentioned that the capillitia of the Myxomycetes and the elaters of the Liverworts serve for the dispersal of the spores. In the case of the Box (*Buxus*), the smooth seeds are forcibly discharged by the contraction of the pericarp, like a bean pressed between the fingers. The dry fruit of *Hura crepitans* bursts apart with a report like that of a pistol, and is scattered in pieces far and wide. The turgescence and elasticity of the cell-walls give rise to the tension which results in the forcible abjection of the sporangia of *Pilobolus* (Fig. 224), and in the ejection of the ascospores of many Ascomycetes. The bursting and rolling up of the segments of the seed-vessels of *Impatiens*, by means of which the dispersal of the seeds is effected, are due to the sudden release of tissue-tensions. The fruits of *Momordica elaterium* and *Ecballium* have the pericarp distended by the pulpy mass within ; when the mature fruit becomes detached from the stalk which fitted like a champagne cork into its place the fluid contents with the seeds are forcibly squirted from the opening.

Germination.—The first condition for successful germination is that the seed should retain its vitality during its dispersal. The small amount of water contained in the seed and the arrest of the main processes of life render the resting seed resistant both to extremes of temperature and to drying. Firm investments serve to protect it from mechanical injury. The second condition of germination is that the seed should reach suitable soil, and this is effected by the assistance of wind, rain, and animals aided by the existence of cracks and crevices in the ground. The fixation of the seed in the soil, which is often of importance for the emergence of the seedling from the testa, is assisted by structural peculiarities of the surface such as furrows, ridges, bristles, and hairs; the latter may be able to expand hygroscopically.

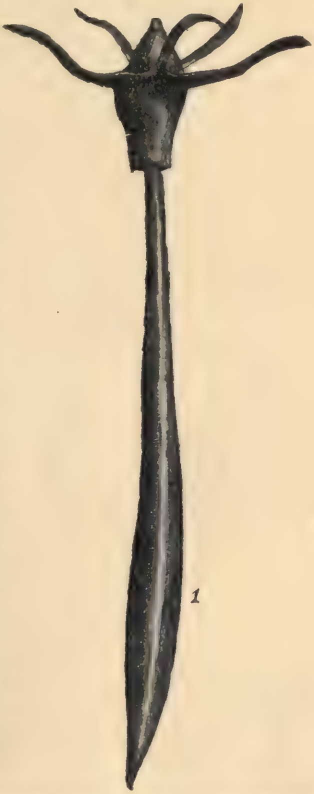


FIG. 250.—*Kandelia Rheedii.* The massive root of the seedling (*1*) has broken out of the fruit. When the plant separates from the fruit the root will become inserted into the muddy soil. (After SCHIMPER'S *Plant-Geography.*)

The fruits of the Geraniaceae (*Erodium*, Fig. 222) and Gramineae (*Stipa*, *Avena sterilis*. and species of *Aristida*) are enabled, by means of movements due to hygroscopic torsion assisted by the presence of stiff backwardly-directed bristles to bury themselves in the ground. In the case of *Trifolium subterraneum* and *Arachis hypogaea* the same result is accomplished by the geotropic growth of the fruit-stalks, while the seed-capsules of *Linaria cymbalaria* are deposited in the crevices of walls and cliffs by the negative heliotropic movements of the fruit-stalks. Nuts, acorns, and seeds buried by squirrels or other animals in the ground and forgotten, or for any reason not made use of, often germinate. The seedlings of Mangrove trees, *Rhizophora*, *Bruguiera*, and *Kandelia* (Fig. 250), exhibit a most peculiar manner of growth to ensure their lodgment in the ground. The seed germinates in the fruit before it is detached from the tree. When the radicle has attained a considerable length, the young seedling, separating either from the cotyledons or from the fruit-stalk, falls to the earth, boring like an arrow into the mud, in which it sticks erect and is thus enabled to commence its growth without delay. In some species of the Mimosaceous genus *Inga* naked embryos are also liberated from the fruits or seeds.

Many seeds and fruits acquire a more or less voluminous MUCILAGINOUS SHEATH, which serves a double purpose. Quince seeds, Flax seeds, seeds of the Plantain, of Crucifers, the fruits of *Salvia horminum*, seed of *Cuphea* and *Cobaea* (in the mucilage cells of which delicate thickening bands are rolled up), afford the best-known examples of such slimy envelopes, which, in addition to fixing the seed to the ground, serve to absorb water by holding it in their substance or drawing it in hygroscopically (cf. Mistletoe berries). Fruit-walls, by their spongy nature, may also serve as water-carriers (ripe fruits of *Tropaeolum*, *Poterium spinosum*, *Medicago terebellum*).

In the soil the seed swells quickly or more slowly and then at once or after a resting period (dependent in part on delay in swelling due to hard seed coats, partly on the time needed for the growth of the embryo) commences to germinate. In some cases the germination (both of seeds and of fungal spores or pollen grains) is dependent on the presence of special substances or of the host plants (*Orobanche*, *Tozzia*, spores of *Bulgaria*) in other cases of light (*Viscum*, *Drosera*, *Pitcairnia mäidifolia*, *Veronica peregrina*, *Nicotiana*). In the case of fern-spores the action of light can be replaced by warmth, and in moss spores by the presence of sugar in the solution. The action of light is on the other hand inhibitory in the germination of *Acanthostachys strobilacea* and *Phacelia tanacetifolia* (123).

The seeds of many Conifers do not germinate for several years; those of the Ash and Hornbeam in 2 and those of *Euphorbia cyparissias* in 4-7 years. Some plants again, in addition to seeds which germinate in the first year, produce others which require a longer rest (*Trifolium pratense*, *Robinia pseudacacia*, *Cytisus Laburnum*, *Reseda lutea*, *Euphorbia exigua*, species of *Dianthus*, etc.). Even under favourable circumstances such seeds do not germinate until a definite length of time has elapsed. Treatment with strong sulphuric acid may in such cases increase the permeability of the seed-coat and hasten germination. Germination may be delayed also by external conditions, and the vitality of the seed may still be retained for years. Thus, for example, on the removal of a forest from land that had been under cultivation for forty-six years, PETER found that a great variety of field-plants at once sprang up as soon as the requirements for their germination were restored. The plants developed under such circumstances are, however, often weakly (124).

Germination, according to the observations of KLEBS, is introduced by true processes of growth, which result in THE RUPTURE OF THE SEED COVERINGS (125). This is effected either by the growing radicle, or, in many Monocotyledons, by the cotyledon. In other seeds enclosed within a shell, the bursting of the latter by the growth of the endosperm or cotyledons precedes germination. In cases where the shell is very hard and does not consist of two halves easily separable by internal pressure (as in Walnuts and Cherry-stones), special places are often provided for the egress of the young seedling.

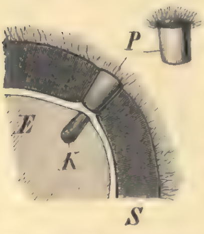


FIG. 251.—Section through the upper part of the fruit of *Acrocomia sclerocarpa*. *S*, The hard shell; *P*, the plug which is pushed out of the shell by the germinating embryo, *K*; *E*, endosperm. (After PFITZER.)

Such places are often present in the thick and hard seed-coats of many palms. At the end of a Coco-nut, for example, three points of egress, behind the thinnest of which the embryo will be found embedded in the endosperm, are very easily seen. Through the extremely hard, thick shell of another Coco-palm, *Cocos lapidea*, there are three long germinal pores, while the seedling of *Acrocomia sclerocarpa* has only to push a loosely fastened plug out of the thick shell of the seed (Fig.

251) (126). Similar contrivances are found in the case of *Pandanus*, *Canna*, *Typha*, *Potamogeton*, and many Dicotyledons (*Tetragonia expansa*, *Medicago*, and some species of *Onobrychis* and *Portulaca*).

SEEDLINGS PENETRATE THE SOIL by means of the elongation of the primary root, or of the hypocotyl, or also, as is the case with many Monocotyledons, through the movements of the geotropic cotyledons. After the descending part is firmly attached to the soil, by either root-hairs or lateral roots, THE UPWARD GROWTH COMMENCES. In this process the cotyledons may either remain within the seed (hypogeal) or unfold above ground (epigeal). The first is often the case where the cotyledons are full of reserve material (*Phaseolus multiflorus*, *Aesculus*, *Quercus*), or where their function is to absorb nourishment from the endosperm (in Palms and the scutellum of Gramineae). More frequently the cotyledons are pushed above ground, and may then be thick and filled with reserve nourishment, or thin and turning green on exposure to the light In many Monocotyledons, as also in *Ricinus*, etc., the cotyledons, even if they afterwards appear above ground, may first take up the nutritive substances of the endosperm; while in the Conifers the cotyledons perform the same office above ground.

THE COTYLEDONS ARE DRAWN FROM THE SEED by the curvature of the hypocotyl or of the petioles of the cotyledons (*Smyrnium*, *Delphinium*). The seed-coverings also are often further ruptured by the swelling of the hypocotyl (Cucurbitaceae, Fig. 231, etc.).

The unfolding of the first leaves above ground is frequently accompanied by a CONTRACTION OF THE ROOT. This is caused by the cortical cells of the root becoming more stretched in a transverse than a longitudinal direction by their turgescence. In consequence of this the root becomes thicker and shortens considerably. The seedling is in consequence drawn deeper into the soil, and its position rendered more secure. Even older plants, particularly those whose leaves form a radical rosette, notwithstanding their upward growth, are held close to the ground through a similar contraction of their roots. The shortening is indicated by the transverse wrinkling of the surface of the root. According to the researches of RIMBACH the shortening amounts to 30 per cent of the length of root in *Allium ursinum*, to 50 per cent in *Arum maculatum*, and even to 70 per cent in *Oxalis elegans* (127).

When its attachment in the soil is properly provided for, and after the first germ-leaves are unfolded, the young plant has acquired the capacity for self-sustenance, its further growth and development being dependent upon its own activity.

PART II

SPECIAL BOTANY

SECTION I

CRYPTOGAMS

SPECIAL BOTANY

SPECIAL BOTANY is concerned with the special morphology and physiology of plants. While it is the province of general botany to investigate the structure and vital processes of the whole vegetable kingdom, it is the task of special botany to interpret the structure and vital processes of its separate divisions. The aim of general morphology is to determine the phylogenetic derivation of the external and internal segmentation of plants, and to refer their numerous structural peculiarities to the primitive form from which they have arisen. The purpose of special morphology, on the other hand, is to trace the development which has been reached in the different divisions of the plant kingdom, to understand the form of individual plants, and to trace the connection between one form and another. Thus the methods of special morphology are also phylogenetic, and furnish the basis for a NATURAL SYSTEM of classification of the vegetable organisms, based upon their actual relationships. Although such a system must necessarily be very imperfect, as it is not possible to determine, directly and indisputably, the phylogenetic connection of different plants, but only to derive indirectly their relationships from morphological comparisons, the aim which we set before us is none the less both legitimate and essentially justified.

Such a natural system, founded on the actual relationship existing between different plants, stands in direct opposition to the ARTIFICIAL SYSTEM, to which has never been attributed more than a practical value in grouping the plants in such a manner that they could easily be determined and classified. Of all the earlier artificial systems, the sexual system proposed by LINNÆUS in the year 1735 is the only one which need be considered.

LINNÆUS, in establishing his classification, utilised characteristics which referred exclusively to the sexual organs, and on this basis distinguished twenty-four classes of plants. In the last or twenty-fourth class he included all such plants as were devoid of any visible sexual organs, and termed them collectively CRYPTOGAMS. Of the Cryptogams there were at that time but comparatively few forms known, and the complicated methods of reproduction of this now large class were absolutely unknown. In contrast to the Cryptogams, the other twenty-three classes were distinguished as PHANEROGAMS or plants whose flowers with their sexual organs could be easily seen. LINNÆUS divided the Phanerogams, according to the sexual character of their flowers, into such as possessed hermaphrodite flowers (Classes I.-XX.), and those in which the flowers were unisexual (XXI.-XXIII.). Plants with hermaphrodite flowers he again divided into three groups: those with free stamens (I.-XV.), which he further distinguished according to the number, mode of insertion, and relative length of the stamens; those with stamens united with each other (XVI.-XIX.); and those in which the stamens were united with the pistil (XX.). Each of the twenty-four classes was similarly subdivided into orders. While some of the classes and orders thus constituted represent naturally related groups, although by the method of their arrangement in the artificial system they are isolated and widely removed from their proper position, they include, for the most part, plants which phylogenetically are very far apart.

LINNÆUS himself (1738) felt the necessity of establishing natural families in which the plants should be arranged according to their "relationships." So long, however, as the belief in the immutability of species prevailed, the adoption of a system of classification expressive of relationship and family could have no more than a hypothetical meaning, and merely indicated a supposed agreement between plants having similar external forms. A true basis for a natural system of classification of organisms was first afforded by the theory of evolution.

The system adopted as the basis of the following description and systematic arrangement of plants is the natural system of ALEXANDER BRAUN, as modified and further perfected by EICHLER, ENGLER, and others.

According to this system, we have to distinguish between CRYPTOGAMS as the lower division, and PHANEROGAMS as the higher division of the plant kingdom.

SECTION I

CRYPTOGAMS

The Cryptogams include an extraordinary variety of the most different plant forms, ranging from unicellular organisms to plants exhibiting segmentation into stem, leaf, and root. The Cryptogams, however, are collectively distinguished from Phanerogams by the mode of their dissemination by SPORES, in contrast to that of the Phanerogams, which is effected by SEEDS; spores are formed also by Phanerogams, but they are not the immediate cause of the origin and development of new individuals. Seeds are multicellular bodies, within which is included the multicellular rudiment or EMBRYO of a plant; while spores, which, in the case of the Cryptogams, become separated from the mother plant, and give rise to a new and independent organism, are unicellular structures. Cryptogams may therefore be termed spore plants or Sporophytes, and Phanerogams seed plants or Spermaphytes; although previous usage and custom would recommend adherence to the older terms.

The Cryptogams are divided into the following main groups:—

I. The Thallophyta, embracing a great variety of plants whose vegetative portion may consist of one or many cells in the form of a more or less branched thallus. Reproduction is both sexual and asexual, but there is usually no definite succession of the two modes of reproduction.

II. The Archegoniatae exhibit a regular alternation of two generations in their life-history. The asexual generation forms spores, and is called the Sporophyte. From the spore the sexual generation or Gametophyte develops; this bears sexual organs of characteristic construction, the male organs being called antheridia, and the female organs archegonia. From the egg-cell contained in the latter, after fertilisation, the sporophyte again arises. The Archegoniatae are divided into

1. The Bryophyta, which include forms with a leaf-like thallus, as well as cormophytic forms, with evident segmentation into stems and leaves. The Bryophytes possess no true roots, and their conducting bundles, when present, are of the simplest structure. The sporophyte is a stalked or unstalked capsule, which lives semi-parasitically on the sexual plant.

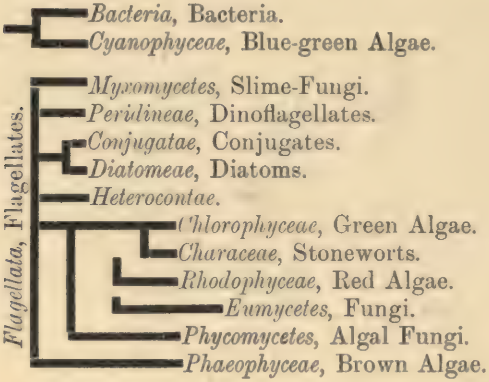
2. The Pteridophyta have small thalloid gametophytes; the sporophytes exhibit a segmentation into stems, leaves, and roots, and also possess true vascular bundles; they thus resemble the Phanerogams in structure.

The Thallophytes and Bryophytes are also characterised as Cellular Plants, in contrast to the Pteridophytes or Vascular Cryptogams, which, together with the Phanerogams, are collectively designated Vascular Plants. Bryophyta and Pteridophyta must be regarded as having had a common origin from the higher Thallophytes, the development of the two groups having been on different lines.

A. I. THALLOPHYTA

It was formerly customary to divide the Thallophyta into Algae, Fungi, and Lichens. The Algae are Thallophytes which possess chromatophores with colouring pigments, particularly chlorophyll; they are, therefore, capable of assimilating and providing independently for their own nutrition. The Fungi, on the other hand, are colourless and have a saprophytic or parasitic mode of life. Such a method of classification, however, although possessing a physiological value, has no phylogenetic significance, as it does not express the natural relationships between the various groups. In the Lichens (Lichenes), which were formerly regarded as simple organisms, the thallus affords an instance of a symbiosis of Algae and Fungi. From a strictly systematic standpoint, the Fungi and Algae composing the Lichens should be classified separately, each in their own class; but the Lichens, among themselves, exhibit such a similarity in structure and mode of life, that a better conception of their characteristic peculiarities is obtained by their treatment as a distinct class.

The phylogenetic connections of the fourteen classes into which the Thallophyta are divided are expressed, so far as is possible, in the following scheme :—


Bacteria, Bacteria.
Cyanophyceae, Blue-green Algae.
Myxomycetes, Slime-Fungi.
Peridineae, Dinoflagellates.
Conjugatae, Conjugates.
Diatomeae, Diatoms.
Heterocontae.
Chlorophyceae, Green Algae.
Characeae, Stoneworts.
Rhodophyceae, Red Algae.
Eumycetes, Fungi.
Phycomycetes, Algal Fungi.
Phaeophyceae, Brown Algae.
Flagellata, Flagellates.

The Bacteria and Cyanophyceae are among the most simply organised Thallophyta; they are closely connected and are often grouped together as the Schizophyta. They occupy an isolated position in contrast to the remaining simple Thallophytes, which with greater or less probability may be derived from the Flagellatae. The Flagellatae used to be (and frequently still are) placed with the lowest animals. As a matter of fact they combine plant and animal characteristics, and may also be regarded as the starting-point of the lower animals. The Myxomycetes may also have sprung from them as a group of colourless saprophytes. The Peridineae are a further-developed branch of the Flagellatae. The simplest forms among the Heterocontae, the Green Algae, and the Phaeophyceae connect directly with the Flagellata; on the other hand a direct connection of the latter with the Conjugatae and Diatomeae (which together form the Zygophyceae), while probable, is not shown in existing forms.

The Phycomycetes have branched off from the main series of the Chlorophyceae. The origin of the Red Algae and the Eumycetes, which appear to have sprung from a common stock, is still in doubt. The Characeae occupy a quite isolated and very advanced position, and are usually regarded as the most highly developed of the Green Algae.

The Thallophytes are commonly multiplied and distributed by asexually produced spores, the mode of development of which differs in the several groups. In many cases the spores arise by a process of cell division within certain cells, which are known as sporangia; in other cases they arise by modification and separation of cells of the thallus or by a process of cell-budding. When the spores possess cilia and are able to move actively in the water, they are known as swarm-spores (zoospores); when they do not bear cilia they are termed aplanospores. In the latter case the spores if distributed by water may be naked, or they may be provided with a cell-wall and suited for distribution in the air.

Sexual reproduction is also of wide-spread occurrence. It consists, in the simplest cases, in the production of a single cell, the ZYGOSPORE or ZYGOTE, by the union or conjugation of two similarly formed sexual cells or gametes. The organs in which the gametes are formed are termed gametangia; planogametes are provided with cilia while aplanogametes are non-ciliated. In many of the more highly developed forms, however, the gametes are differentiated as small, usually ciliated, male cells or SPERMATOZOIDS, and as larger non-ciliated female cells, the egg-cells or OOSPHERES. The spermatozoids are formed in antheridia, the oospheres in oogonia. As a result of the fusion of an egg-cell and a spermatozoid, an OOSPORE is produced. The first form of sexual reproduction or fertilisation is termed ISOGAMOUS, the second OOGAMOUS; but these are connected by intermediate forms. It must be assumed that the sexual cells have been derived in the phylogeny of plants from asexual spores, and that asexual multiplication has taken origin from simple cell division. The gametangia, oogonia, antheridia, and sporangia of the Thallophyta are homologous structures. The sexual reproduction has originated independently in several distinct groups.

While the reproduction of some Thallophyta is exclusively asexual, and of others exclusively sexual, in many others both forms of reproduction occur. In the latter case this may occur on the one plant, or separate successive generations may be distinguishable. Generally speaking, there is, however, no regular succession of asexual and sexual generations in Thallophytes, the mode of reproduction being to a great extent under the influence of external conditions (1). Only in some Brown Sea-weeds, in the Red Sea-weeds, and some Fungi is there an alternation of a sexual generation (gametophyte) with an asexual (sporophyte), such as is found in all Bryophytes and Pteridophytes.

CLASS I

Bacteria (2)

Bacteria are unicellular or filamentous organisms of very simple construction. Chlorophyll is wanting in them, and their mode of life is consequently a parasitic or saprophytic one. A large number of species exist distributed over the whole earth, in water, in the soil, in the atmosphere, or in the bodies of dead or living plants and animals. They are often termed Fission-Fungi, or Schizomycetes, since the multiplication of the unicellular forms takes place by a division into two and the separation of the segments. This mode of multiplication is also found in other unicellular plants.

The cells of the Bacteria are surrounded by a thin membrane, and contain a protoplasmic body, which is usually colourless, and can be made to contract away from the membrane by plasmolysis. The protoplasm may contain one or more vacuoles. One or several granular structures are also present in the protoplast; these so-called chromatin bodies may be deeply coloured by stains, and have been regarded as nuclei by various authors. Since, as yet, undoubted karyokinetic division has not been observed in these bodies, the presence of nuclei in the bacterial cell cannot be regarded as certainly established.

For the most part the Bacteria are extraordinarily minute organisms, and probably include the smallest known living beings. The spherical cells of the smallest forms are only 0·0008 mm. in diameter; the rod-shaped cells of the tubercle bacillus are only 0·0015-0·004 mm. long, while the transverse diameter of most species is about 0·001 mm.

The simplest form of Fission-Fungi are represented by minute spherical cells, COCCI. Forms consisting of rod-shaped cells are designated BACTERIUM or BACILLUS. Rod-shaped forms with a slight spiral curvature are called VIBRIO, and those more strongly curved SPIRILLUM. Straight filamentous forms are termed LEPTOTHRIX, spirally wound filaments, SPIROCHAETE. In the highest stage of their development the Fission-Fungi consist of cell filaments exhibiting false branching. The unicellular cocci, rod-shaped forms, and vibrios may also remain united in chains after the cell-division. Frequently the cell-membranes undergo a mucilaginous swelling, the cells or cell-rows being embedded in the gelatinous mass. This stage of development is termed ZOOGLOEA.

Many Bacteria are motile. Their independent movements are due to the vibration and contraction of fine protoplasmic cilia. These flagella, according to A. FISCHER, are either distributed over the whole surface of the cells (peritrichous) (*e.g. Bacillus subtilis*, Fig. 254 *a*, *d*; *Bacillus typhi*, Fig. 252 *c*; *Bacillus tetani*, Fig. 257 *e*), or they spring from a single point either as a single flagellum (monotrichous) or as a group (lophotrichous). A single, polar flagellum occurs in *Vibrio cholerae* (Fig. 252 *a*); a polar terminal tuft of flagella in *Spirillum undula* (Fig. 252 *b*, *d*); a lateral tuft in the swarm-spores of *Cladothrix* (Fig. 253). The ciliary tufts may become so closely intertwined as to present the appearance of a single thick flagellum. The cilia are never drawn within the body of the cell, but undergo dissolution before the formation of spores takes place, or under unfavourable conditions (Fig. 252 *e*).

Multiplication of the individual is accomplished vegetatively by the active division or fission of the cells; the preservation and distribution of the species by the asexual formation of resting spores. These arise as endospores (Figs. 254 *c*, 256 *e*, *f*) in the middle or at one end of a cell by the inner portion of the protoplasm separating itself from the peripheral, and surrounding itself with a thick membrane. The membrane of the mother cell becomes swollen and disintegrated when the spore is ripe. Spores are not found in all species.

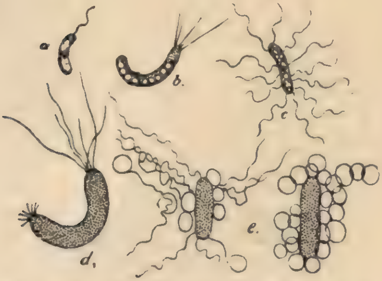


FIG. 252.—Types of arrangement of flagella. *a*, *Vibrio cholerae*; *b*, *d*, *Spirillum undula*; *d*, development of a new bunch of cilia in division; *c*, *Bacillus typhi*; *e*, *Bacillus subtilis*. (After A. FISCHER, × 2250.)

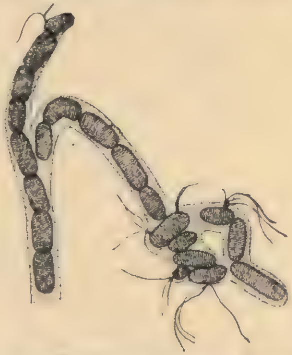


FIG. 253.—*Cladothrix dichotoma*. Formation of swarm cells from the cells of the filament. (After A. FISCHER, × 1000.)

Bacillus subtilis, the Hay bacillus (Fig. 254), which appears as a rule in the decoction obtained by boiling hay in water, will afford an example of the life-history of a Bacterium. The spores of this species, which withstand the effect of the boiling water, produce on germination rod-shaped swarming cells with cilia on all sides; these divide and may remain connected in short chains. At the surface of the fluid these swarming cells change into non-motile cells without cilia, which divide up, giving rise to long intertwined chains of cells. These are associated together in the pellicle covering the surface (zoogloea stage). Spore formation occurs when the nutritive substances in the fluid are exhausted.

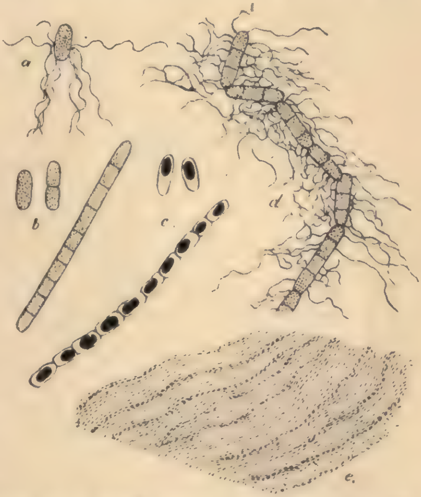


FIG. 254.—*Bacillus subtilis*. *a*, *d*, Motile cells and chain of cells; *b*, non-motile cells and chains of cells; *c*, spores from the zoogloea, *e*. (From A. FISCHER, *Vorles. über Bacterien*. *a*-*d*, × 1500; *e*, × 250.)

Although the cycle of forms passed through in the life-history of a Bacterium is a very simple one, the individual species, which can often be barely distinguished by morphological characters, show great variety in their metabolic processes and in their mode of nutrition. The majority of Bacteria require oxygen for their respiration, and are therefore aerobic; many can, however, develop without this gas, while some species, *e.g.* the butyric acid bacterium and the tetanus bacillus, are strictly anaerobic and only succeed in the absence of oxygen (cf. p. 242).

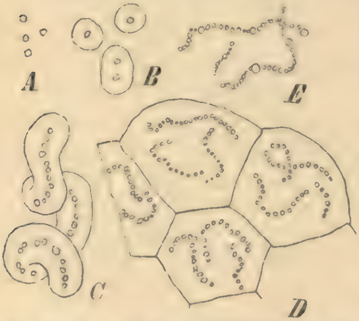


FIG. 255.—*Leuconostoc mesenterioides.* *A*, Isolated cells without gelatinous sheath; *B*, *C*, formation of chain of cells with gelatinous sheath; *D*, portion of mature zoogloea; *E*, formation of isolated cells in the filaments of the zoogloea. (After VAN TIEGHEM, × 520.)

Saprophytic and parasitic species are distinguished, though a sharp separation is often impossible. In cultures the parasitic forms can be made to lead a saprophytic life on suitable substrata.

To the saprophytic Bacteria belong in the first place the forms which inhabit water. The widely distributed *Cladothrix dichotoma* is morphologically the highest among these. It is found in stagnant water, and consists of falsely branching delicate filaments attached to Algae, stones, and woodwork, and forming a slimy coating over them; the filaments are composed of rod-shaped cells. Reproduction is effected by ciliated swarm-cells, which originate by division from cells of the filament and are set free by the swelling of the sheath (Fig. 253). The swarm-cells come to rest after a time and grow into new filaments.

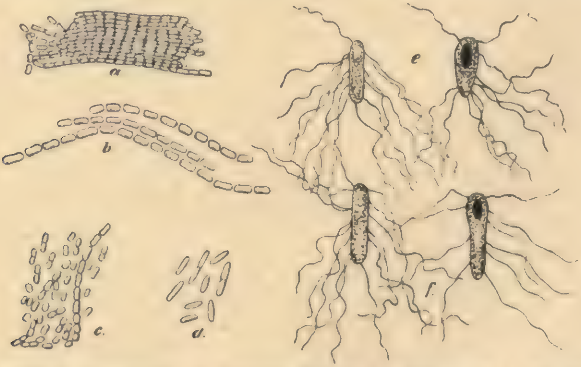


FIG. 256.—Bacteria of fermentation. *a-c*, Vinegar bacteria; *a*, *Bacillus aceti*; *b*, *Bac. Pasteurianus*; *c*, *Bac. Kutzingianus*; *d*, *Bac. acidi lactici*, lactic acid bacillus; *e*, *Clostridium butyricum*, butyric acid bacillus; *f*, *Plectridium paludosum*, fermentation bacterium from marsh water. (From A. FISCHER, *Vorles. über Bacterien*, × 1000.)

Another very common form is *Crenothrix Kühniana*, which consists of unbranched filaments attached to the substratum, but easily broken. It often forms masses in the cavities of water-pipes, blocking them up and rendering the water undrinkable. The reproduction of *Crenothrix* is effected by small, round, non-motile cells, which arise by subdivision of the cells of a filament enclosed by its sheath.

The numerous kinds of Sulphur Bacteria, of which *Beggiatoa alba* is the most widely distributed, are found in sulphurous springs and at the bottom of pools where sulphuretted hydrogen is being formed by decomposition of organic material. These Bacteria oxidise sulphuretted hydrogen into sulphur, and store the latter substance in the form of rounded granules within their cells (cf. p. 243).

Leptothrix ochracea, the so-called Iron-Bacterium, oxidises oxide of iron to the hydrated oxide of iron which it accumulates in the sheaths of its filaments (cf. p. 243). It occurs in ditches and swampy places in meadows.

The zymogenous or fermentation Bacteria and the saprogenous or decomposition Bacteria are other saprophytic forms. The former oxidise or ferment carbohydrates. The latter decompose nitrogenous animal or vegetable substances (albumen, meat, etc.) with the liberation of ill-smelling gases.

Thus *Leuconostoc mesenterioides* (Fig. 255) causes fermentation of beet-sugar. It forms large mucilaginous masses like frog-spawn, the bead-like rows of cells being surrounded by a gelatinous investment. The acetic acid bacteria (Fig. 256 *a*, *b*, *c*) oxidise alcohol to acetic acid. The transformation of sugar into lactic acid is brought about by the rod-like cells of *Bacillus acidi lactici* (Fig. 256 *d*). *Clostridium butyricum* (Fig. 256 *e*) forms butyric acid from various carbohydrates in the absence of oxygen, while certain marsh Bacteria (Fig. 256 *f*) in the absence of oxygen form marsh-gas from cellulose. *Bacillus vulgaris* is the most common cause of decomposition of meat, albumen, etc.

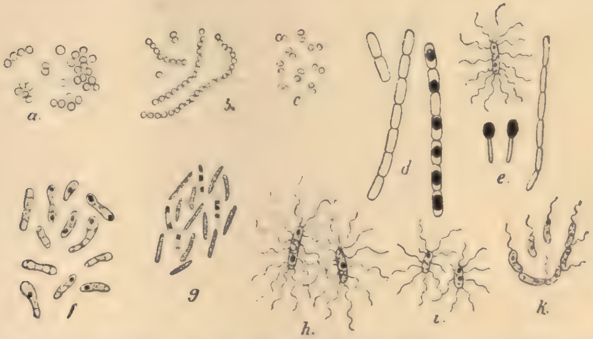


FIG. 257.—Pathogenic Bacteria. *a*, Pus cocci ; *b*, erysipelas cocci ; *c*, gonorrhœa cocci ; *d*, splenic fever bacilli ; *e*, tetanus bacilli ; *f*, diphtheria bacilli ; *g*, tubercle bacilli ; *h*, typhoid bacilli ; *i*, colon bacilli ; *k*, cholera bacilli. (From A. FISCHER, *Vorles. über Bacterien*, × about 1500.)

The photogenic bacteria produce within their cells a substance which becomes phosphorescent on oxidation (cf. p. 246). The most widely spread of these phosphorescent bacteria is *Bacterium phosphoreum*, and occurs on meat (79).

The parasitic bacteria inhabit both animals and plants. The best known forms which cause diseases of plants (bacterioses) are *Pseudomonas Hyacinthi*, *Bacillus phytophthorus*, which attacks the potato, and *Bacillus Oleae*, which gives rise to the Canker of the Olive Tree (3).

The numerous pathogenic Bacteria are the most important causes of infectious diseases. Their injurious influence on the tissues and blood of men and animals is brought about by the excretion of poisonous substances, to which the name toxins has been given. The following forms may be mentioned. *Staphylococcus pyogenes* (Fig. 257 *a*), the cocci of which form irregular or racemose masses, is the most common cause of suppuration, while *Streptococcus pyogenes* (Fig. 257 *b*), with cocci united in chains, occurs in erysipelas and other suppurative lesions. *Micrococcus* (*Diplococcus*) *gonorrhoeae* (Figs. 257 *c*, 258 *a*), has somewhat flattened cocci arranged in pairs, and causes gonorrhœa. *Bacillus anthracis* (Figs. 257 *d*, 258 *c*) was found by R. KOCH in the blood and organs of animals suffering from splenic fever. The relatively large rod-shaped cells may be united in short chains; they form endospores in cultures in the same way as the Hay bacillus. *Bacillus tetani* (Fig. 257 *e*) occurs in the soil, and is the cause of tetanus. Its straight rod-shaped cells are ciliated, and grow only in the wound itself; their spores are formed in the swollen end. *Bacillus influenzae*, short, slender rods; *Bacillus pestis*, small, stout, non-motile rods. LÖFFLER'S *Bacillus diphtheriae* (Fig. 257 *f*) consists of small rod-shaped cells sometimes thickened at one end. KOCH'S *Bacillus tuberculosis* (Figs. 257 *a*, 258 *b*), which is found in all tuberculous lesions and secretions, as in the sputum, is a slender, slightly curved rod. Typhoid fever is caused by the ciliated cells of *Bacillus typhi* (Fig. 257 *h*); *Bacillus coli* (Fig. 257 *i*), the colon bacillus, which is as a rule harmless and always occurs in the human intestine, closely resembles the typhoid bacillus. The comma bacillus of Asiatic cholera, *Vibrio cholerae* (Fig. 257 *k*), was discovered by R. KOCH. It occurs in the intestine as short curved rods with a single polar flagellum, and sometimes in longer chains of spirally wound cells. *Spirochaete obermeieri*, which consists of long, thin, spirally wound filaments, without flagella, but capable of motion, occurs in the blood during the attacks of relapsing fever, of which it is the cause.

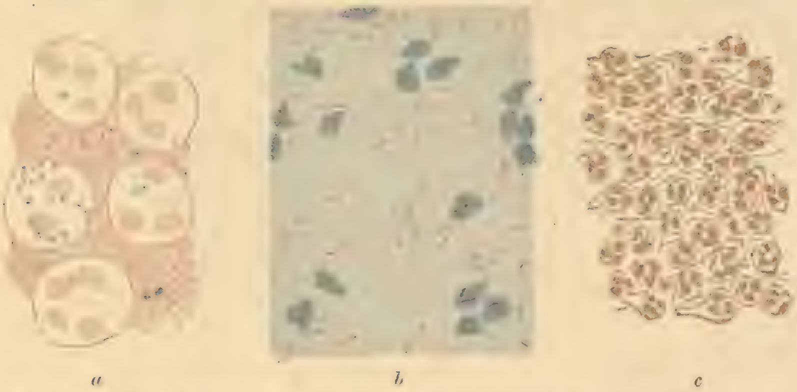


FIG. 258.—Stained preparations from Ziegler's *Text-book of Pathology*. *a*, gonococci in the gonorrhœal discharge, mucus and pus corpuscles with cocci (methylene blue and eosin), × 700; *b*, tubercle bacilli in sputum of phthisis (fuchsin and methylene blue), × 400; *c*, splenic fever bacilli in the pustule of the disease (methylene blue and vesuvin) × 350. (From A. FISCHER, *Vorles. über Bacterien.*)

Besides the above injurious parasites there are others which are more or less harmless occurring on the mucous membranes, in the mouth (Fig. 4), or the intestine. *Sarcina ventriculi*, which occurs as packets of cocci in the stomach and intestine of man, will serve as an example of these.

The Bacteria included under the name *Bacillus radicicola* (=*Rhizobium Leguminosarum*) occur in the root-tubercles of Leguminosae, and, like certain other Bacteria found in the soil (*Azotobacter chroococcum*), and in the sea, are capable of utilising free nitrogen in their metabolism (p. 232). The denitrifying Bacteria which occur in the soil and in the sea decompose nitrates and nitrites, and liberate free nitrogen.

In addition to saprophytic and parasitic Bacteria, there are some which, though possessing no chlorophyll, obtain their food from inorganic compounds only. These are the Nitrite Bacteria (*Nitrosomonas*), and the Nitrate Bacteria (*Nitrobacter*), which live in the soil. The former oxidises ammonia to nitrous acid, and the latter oxidises the nitrous to nitric acid. They both obtain their carbon from carbonic acid, and thus derive their food independently of any organic food-supply (Fig. 259, cf. p. 217).

The Myxobacteriaceae (4) are a very peculiar family of Bacteria, our accurate knowledge of which is in the first instance due to THAXTER. They nearly all live saprophytically on the dung of animals, and in habit resemble the Myxomycetes (cf. p. 340). In the vegetative stage they appear as swarms of rod-shaped Bacteria connected together by the gelatinous substance secreted by the cells, and exhibit slow creeping movements. Ultimately they form fructifications that are usually brightly coloured ; these have the form either of definitely limited masses of spores or of cysts containing within a firm membrane the numerous spores. The cysts are unstalked, or are raised singly or in groups on a stalk, formed, like the wall of the cyst, of the hardened gelatinous material (Fig. 260).

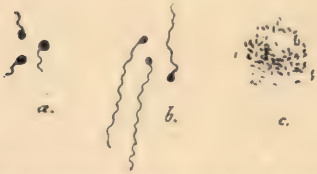


FIG. 259.—Nitrifying bacteria, after Winogradsky. *a*, *Nitrosomonas europaea*, from Zurich ; *b*, *Nitrosomonas javanensis*, from Java ; *c*, *Nitrobacter*, from Queto. (From FISCHER, *Vorles. über Bacterien*, × 1000.)

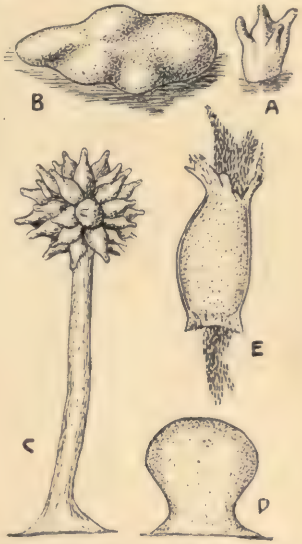


FIG. 260.—*A*, *Myxococcus digitatus*, bright red fructification occurring on dung (× 120). *B*, *Polyangium primigenium*, red fructification on dog's dung (× 40). *C*, *Chondromyces apiculatus*, orange fructification on antelope's dung. *D*, young fructification (× 45). *E*, single cyst germinating (× 200). (*A*, *B*, after QUEHL ; *C-E*, after THAXTER.)

CLASS II

Cyanophyceae, Blue-green Algæ (5)

The Cyanophyceae are simply organised unicellular or filamentous Thallophytes of a bluish-green colour ; the cells or filaments are frequently united into colonies by the gelatinous swelling of the cell walls. The numerous species, which are distributed over the earth, live in water, or form gelatinous or filamentous growths on damp soil, damp rocks, or the bark of trees.

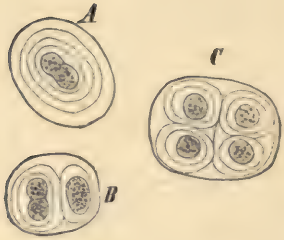


Fig. 261.—*Gloeocapsa polydermatica.* *A*, In process of division; *B*, to the left, shortly after division; *C*, a later stage. (× 540.)

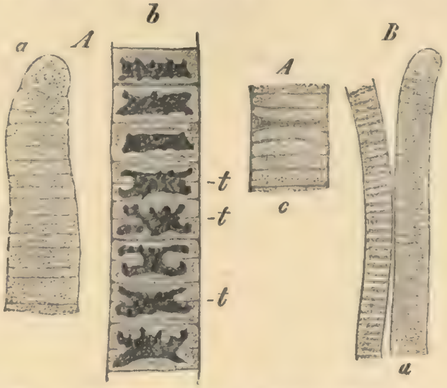


Fig. 262.—*A*, *Oscillaria princeps*: *a*, terminal portion of a filament; *b*, portions from the middle of a filament properly fixed and stained; *t*, cells in division (× 1080). *B*, *Oscillaria Froelichii* (× 540).

The protoplast of each cell possesses a peripheral chromatophore of the form of a hollow cylinder or hollow sphere; in addition to chlorophyll this contains a blue-green pigment phycocyan from which the name of the class is derived. The product of assimilation is glycogen. The centre of the cell is occupied by the colourless central body, which corresponds to a nucleus and in vegetative cells is in a condition of continuous mitotic division. As definite inclusions of the cells may be mentioned the cyanophycin granules, which serve as reserve material and are situated in the neighbourhood of the transverse septa or within the chromatophore, and the mucilage spheres which appear in close proximity to the nucleus. Chitin has been shown to be present in the cell wall.

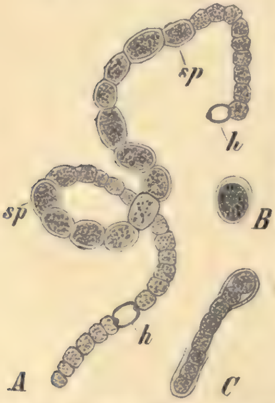


Fig. 263.—*Nostoc Linckii.* *A*, Filament with two heterocysts (*h*) and a large number of spores (*sp*); *B*, isolated spore beginning to germinate; *C*, young filament developed from spore. (After Bornet, × 650.)

Reproduction is exclusively vegetative by cell division. In many forms resting spores are formed by the enlargement of single cells, the walls of which become greatly thickened (Fig. 263). Resting nuclei are present in these spores.

Just as the Bacteria are designated Fission-Fungi (Schizomycetes), the Blue-green Algae may be termed Fission-Algae (Schizophyceae), since the reproduction of both depends on fission. The two groups would form the class of fission plants Schizophyta. The Bacteria and the Cyanophyceae have much in common, but the cilia and endospores of the former are unknown in the latter group. According to the observations of PHILIPPS, which, however, require confirmation, some of the Cyanophyceae which exhibit movements possess cilia.

The simplest Cyanophyceae consist of spherical cells ; this is the case with species of *Chroococcus.* In *Gloeocapsa* (Fig. 261), found on damp rocks and walls, the cells remain connected together after division into a gelatinous mass, forming a multicellular colony.

The species of *Oscillaria,* which occur everywhere in water or on damp soil, are the simplest of the filamentous forms. The filament, which is usually provided with a thick sheath, consists of similar flattened cells (Fig. 262). It can separate into pieces (hormogonia), which become free owing to the pressure of the sheath, and grow into new filaments. In other filamentous Cyanophyceae specially modified cells with their contents degenerated occur in the filament. The significance of these heterocysts is not yet clear. The species of *Nostoc* (Fig. 263), whose bead-like filaments are united by the swelling of the cell-walls into more or less spherical gelatinous colonies living on damp soil or in water, afford an example of this.

Many Cyanophyceae take part with the Fungi in the formation of Lichens. Some species also are endophytic and inhabit cavities in other plants, *e.g. Anabaena* in *Azolla, Nostoc* in some Liverworts, in *Lemna,* and in the roots of *Cycas* and *Gunnera.*

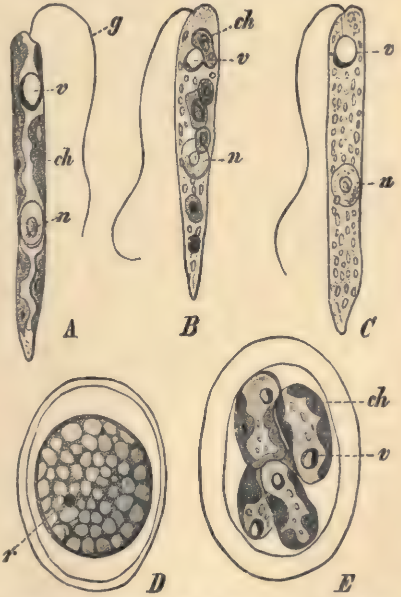


FIG. 264.—*Euglena gracilis. A,* Form with green chromatophores (*ch*) ; *n,* nucleus ; *v,* vacuole and red eye-spot ; *g,* flagellum. *B,* Hemisaprophytic form with small green chromatophores. *C,* Colourless saprophytic form occurring in nutrient solution in absence of light. *D,* Resting cyst of the form *C* ; *r,* red eye-spot. *E,* Germination of the resting cyst of the form *A* by division into four daughter cells which later escape. (After ZUMSTEIN ; *A, C,* ×630 ; *B,* ×650 ; *D, E,* ×1000.)

Class III

Flagellata (Flagellates)

(6, 7)

The Flagellata are a group of unicellular, aquatic organisms exhibiting a wide range of form ; they combine animal and vegetable characteristics, and may be regarded as the starting-point on the one side of unicellular Thallophytes, on the other of the Protozoa.

The protoplast exhibits contractile or amœboid movements, and is limited by a denser protoplasmic layer and not by a definite cell wall. One or more cilia (flagella) are present as motile organs. The protoplast contains a nucleus, a pulsating vacuole, and in many species well-formed green, yellow, or brownish-yellow chromatophores. Other forms are colourless and live saprophytically ; many are also able to take up solid particles as food.

Most representatives of the group live as naked, free cells; others form more or less complicated cell-colonies held together by mucilage, or they possess peculiar stalked or unstalked firm investments.

Sexual reproduction is wanting. Multiplication takes place by longitudinal division, and in many species thick-walled resting spores or cysts are produced.

Euglena (Fig. 264) may be taken as an example. The species live in water containing organic substances and often appear in large numbers. By varying the nutritive conditions colourless forms with reduced chromatophores are obtained (8).

CLASS IV

Myxomycetes (Slime-Fungi) (9)

The Myxomycetes form an independent group of lower Thallophytes; in certain respects they occupy an intermediate position between plants and animals, and have in consequence also been termed Mycetozoa or Fungus-animals. They are represented by numerous species, and are widely distributed over the whole earth. In their vegetative condition the Slime-Fungi consist of naked masses of protoplasm, the PLASMODIA, containing numerous small nuclei but utterly devoid of chlorophyll. Glycogen occurs as a reserve substance, while starch is not found. The plasmodia (p. 54) are found most frequently in forests, upon soil rich in humus, upon fallen leaves, and in decaying wood. They creep about on the substrata, changing their form at the same time, and thrust out processes or pseudopodia, which may in turn coalesce. At the period of spore-formation the plasmodium creeps out from the substratum towards the light and air, and, after coming to rest, is converted into single or numerous and closely contiguous fructifications, according to the genus. On the periphery of each fructification an outer envelope or PERIDIUM is formed; while internally the contents of the fructification separate into spores, each of which is provided with a nucleus, and enclosed by an outer wall. The isolation of the spores may take place on the conclusion of cell divisions (*Trichia*); in other cases (*e.g. Fuligo*) the plasmodium divides into a number of multinucleate portions while nuclear division is in progress, and these portions subsequently divide, giving rise to the spores. The spores thus formed have accordingly an asexual origin. In many genera, part of the internal protoplasm within the SPORANGIUM or spore-receptacle is utilised in the formation of a CAPILLITIUM (Fig. 266 *B*), consisting of isolated or reticulately united threads or tubes. Upon the maturity of the spores, the peridium of the sporangium becomes ruptured, the capillitium expands (Fig. 265 *B*), and the spores are dispersed by the wind, aided by the hygroscopic movements of the capillitium. In the case of the genus *Ceratiomyxa*, the process is somewhat simplified, as the fructification is not enveloped by a peridium, and the spores are produced at the extremities of short stalks. SEXUAL REPRODUCTION is entirely absent in the Myxomycetes.

A good example of the development of the plasmodia from the spores is afforded by *Chondrioderma difforme*, a Slime-Fungus common on decaying leaves, dung, etc., upon which it forms small, round, sessile sporangia. The germination of the spores (Fig. 59 *a*) may be easily observed when cultivated in an infusion of Cabbage leaves or other vegetable matter. The spore-wall is ruptured and left empty by the escaping protoplast. After developing a flagellum or CILIUM as an organ of motion, the protoplast swims about in the water, being converted into a SWARM-SPORE (Fig. 59 *e-g*), with a cell-nucleus in its anterior or ciliated end, and a contractile vacuole in the posterior end of its body. Eventually the cilium is drawn in, and the swarm-spore becomes transformed into a MYXAMOEBA; these have the capacity of multiplication by division. In conditions unfavourable for their development they surround themselves with a wall, and as MICROCYSTS pass into a state of rest from which, under favourable conditions, they again emerge as swarm-spores. Ultimately a number of the myxamoebae approach close together (Fig. 59 *l*) and coalesce, forming small plasmodia (Fig. 59 *m*), which in turn fuse with others into larger plasmodia (Fig. 59 *n*); no nuclear fusion accompanies this coalescence. Both the amoebae and plasmodia are nourished by the small food particles taken up by the protoplasm, which also exhibits active, internal, streaming movements. After an interval of a few days the plasmodium creeps to the surface of the substratum, and passing into a resting stage becomes at length converted into a white sporangium with a double wall, consisting of an outer, calcareous, brittle peridium and an inner and thinner enveloping pellicle which, in addition to the numerous spores, encloses also a poorly developed capillitium.

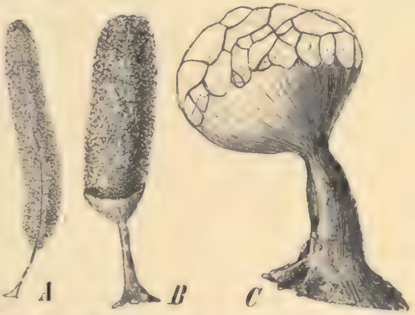


Fig. 265.—Ripe fructifications, after discharge of the spores. *A*, *Stemonitis fusca* (× 10); *B*, *Arcyria punicea* (× 12); *C*, *Cribraria rufa* (× 32).

The development of the other Myxomycetes is accomplished in a similar manner. Very large plasmodia, often over a foot in breadth, of a bright yellow colour and creamy consistency, are formed by *Fuligo varians* (*Aethalium septicum*), and as the "flowers of tan" are often found in summer on moist tan bark. If exposed to desiccation, the plasmodia of this Myxomycete pass into a resting state, and become converted into spherical or strand-like SCLEROTIA, from which a plasmodium is again produced on a further supply of water. Finally, the whole plasmodium becomes transformed into a dry cushion or cake-shaped fructification of a white, yellowish, or brown colour. The fructification, in this instance, is enveloped by an outer calcareous crust or rind, and is subdivided by numerous internal septa. It encloses numerous dark violet-coloured spores, and is traversed by a filamentous capillitium, in which are dispersed irregularly-shaped vesicles containing granules of calcium carbonate. A fructification of this nature, or so-called æthalium, consists, therefore, of a number of sporangia combined together, while in most of the Myxomycetes the sporangia are simple and formed singly. The swarm-spores and myxamoebae of the Myxomycetes indicate an origin of the group from organisms resembling the Flagellata.

The structure and nature of the sporangia afford the most convenient means of distinguishing the different genera. The usually brown or yellow sporangia are spherical, oval, or cylindrical, stalked (Figs. 265, 267) or not stalked (Fig. 266). They usually open by the rupture of the upper portion of the sporangium walls, the lower portion persisting as a cup (Figs. 265 *B*, 266 *A*). In *Cribraria* (Fig. 265 *C*) the upper part of the wall of the sporangium, which contains no capillitium, becomes perforated in a sieve-like manner. In *Stemonitis* (Fig. 265 *A*) the whole peridium falls to pieces, and the capillitium is attached to a collumella, which forms a continuation of the stalk.

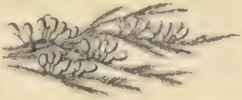


FIG. 267. — *Leocarpus fragilis.* Groups of sporangia upon a Moss. (Nat. size.)

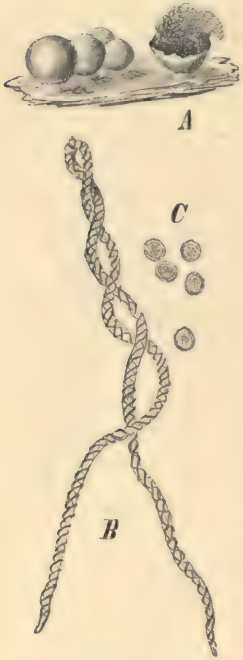


FIG. 266. — *Trichia varia.* *A*, Closed and open sporangia (× 6); *B*, a fibre of the capillitium (× 240); *C*, spores (× 240).

Plasmodiophora Brassicae (10), one of the few parasitic Myxomycetes, causes tuberous swellings on the lateral roots of various species of *Brassica*. Its multinucleate myxamoebae occur in numbers in the cells of the hypertrophied parenchyma of these swellings; after the contents of the host-cell have been exhausted they fuse into plasmodia, and these, eventually dividing into numerous spores, are set free by the disorganisation of the plant. According to PROWAZEK the plasmodium first divides into uninucleate cells which then conjugate in pairs to give rise to the spores; the nuclei before the fusion have undergone a reduction division. The spores germinate like those of *Chondrioderma*, and the myxamoebae penetrate the roots of a young Cabbage-plant. The formation of true sporangia, however, does not take place, and this Slime-Fungus represents a more simply organised or, in consequence of its parasitic mode of life, a degenerate Myxomycete.

CLASS V

Peridineae (6, 11)

The Peridineae or Dinoflagellata are connected as an independent and further developed group with certain Flagellata (Cryptomonadinae). They occur as unicellular, free-swimming organisms in fresh water, but for the most part in the sea where, together with the Diatomeae, they constitute an important constituent of the plankton. Their cells are characterised by the possession of two long cilia or flagella which spring from the middle of the ventral surface in a longitudinal furrow; one of the cilia is directed backwards, the other is thrown into curves and lies in a transverse furrow (Fig. 268 *A*, *gf*). The protoplast contains a nucleus, vacuoles of different sorts, and numerous brownish-yellow chromatophores; the latter contain a mixture of several special pigments (reddish-brown phycopyrin, red peridinin, and yellowish-green chlorophyllin). Oil is usually formed as the product of assimilation. While the Gymnodineae (Fig. 268 *A*) have either naked cells or cells limited by a uniformly thickened cellulose wall, the typical Peridineae have a wall composed of cellulose formed of polygonal plates; these are usually delicately sculptured and perforated with pores. The transverse furrow is formed by one girdle-shaped plate (Fig. 268 *B*).

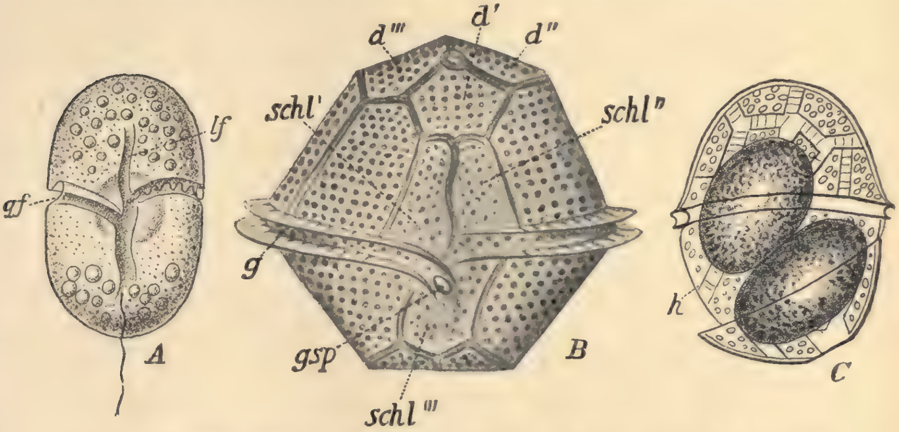


FIG. 268.—*A*, *Gymnodinium rhomboides*: *lf*, longitudinal groove; *gf*, transverse groove. *B*, *Goniodoma acuminatum*: the flagella, which arise from the orifice *gsp*, are not represented; *schl*, *d*, plates of the wall; *g*, girdle. *C*, *Peridinium tabulatum*: *h*, wall. (*A*, *B*, After SCHÜTT; *C*, after KLEBS; from OLTMANN'S *Algae*.)

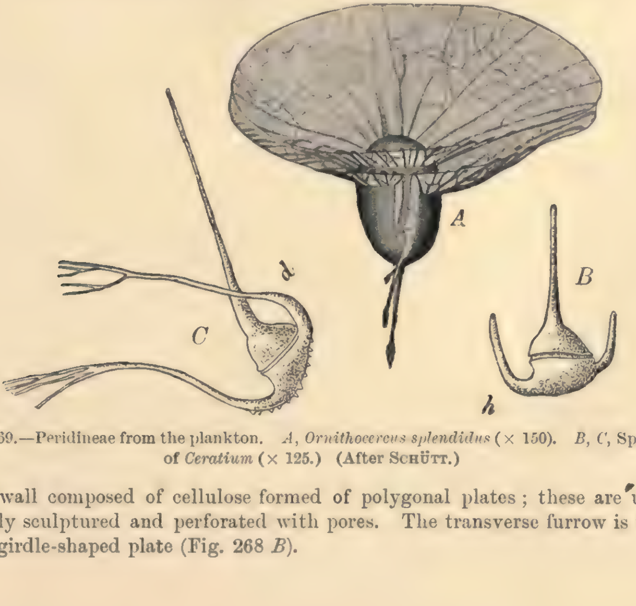


FIG. 269.—Peridineae from the plankton. *A*, *Ornithocercus splendidus* (× 150). *B*, *C*, Species of *Ceratium* (× 125.) (After SCHÜTT.)

In many Peridineae of the plankton the plates bear special wing-like expansions (Fig. 269 *A*) or the cells have long horn-like processes. These adaptations enable the organisms to remain floating in the water ([12]).

In some Peridineae the chromatophores are only represented by colourless leucoplasts. Such species live either as saprophytes or in the same way as animals. *Gymnodinium hyalinum* is a colourless, naked, fresh-water form, the protoplast of which for the purpose of absorbing nourishment loses its cilia and assumes the form of an amœba; in this condition it encloses and digests small Algae ([13]).

Reproduction is by cell-division and also by means of swarm-spores. In the latter case the protoplast escapes from the membrane and either shortly forms a new wall or divides into several swarm-cells (Fig. 268 *C*). Thick-walled resting cells (cysts) also occur. ZEDERBAUER has recently observed a process of sexual reproduction (the conjugation of protoplasts escaping from two similar cells to form a zygote) in *Ceratium* ([14]).

CLASS VI

Conjugatae ([6, 15])

This class of green freshwater Algae includes unicellular and simply filamentous forms, and is clearly distinct from that of the Chlorophyceae. The Conjugatae are most nearly related to the Diatomeae, with which they might be united in the group of the Zygophyceae, since the two classes show essential agreement in their mode of sexual reproduction. This consists in the conjugation of two equivalent gametes to form a zygote or zygospore. Asexual reproduction by means of swarm-spores is wanting in both classes, and since the gametes also are unprovided with cilia these forms are also classed as Acontae. The cells of the Conjugatae which increase in number by cell-division are uninuclear, and differ from those of the Diatoms in having a cell-wall which is not silicified and in the presence of large green chloroplasts of complicated structure.

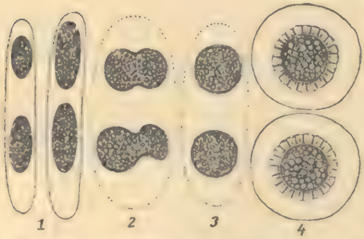


FIG. 270.—*Spirotaenia condensata*. *1*, Conjugating cells each divided into two daughter cells; *2*, *3*, stages of conjugation; *4*, mature zygotes. (After ARCHER; from OLTMANNS'S *Algae*.)

1. The **Mesotaeniaceae**, the simplest of the unicellular Conjugatae, include only a few genera. They are distinguished from the following order by the cell-wall of the shortly cylindrical cells not being formed of two halves. The mode of conjugation presents some differences. In *Spirotaenia* (Fig. 270) the protoplasts of the conjugating cells first divide and the daughter cells unite in pairs to form the

zygotes ; in *Mesotaenium* and *Cylindrocystis* the protoplasts conjugate without a preliminary cell-division. Similar differences are shown by the Diatomeae. The zygote on germination divides into four new individuals.

2. The **Desmidiaceae** are unicellular or their cells are united in rows ; they are of great beauty and, like the Diatoms, exhibit a great variety of form. Their cells are composed of two symmetrical halves, separated, as a rule, from each other by a constriction. Each half contains a large, radiate chromatophore, or a number of plate-like chromatophores united into one. Within the chromatophores are disposed several pyrenoids, while the nucleus lies in the centre of the cell in the constriction. The cells themselves display a great diversity of form and external configuration, being sometimes rounded (*e.g. Cosmarium*, Fig. 271 *A*, *B*) sometimes stellate (*Micrasterias*, Fig. 271 *D*). The cell walls, which, as in the Diatoms, consist of separate halves, are frequently beset with wart- or horn-like protuberances and often provided with pores. In some genera there is no constriction between the two halves of the cell. This is the case, for instance, in the crescent-shaped *Closterium moniliferum* (Fig. 272 *F*), whose two chromatophores consist of six elongated plates, united in the long axis of the plant, while in each end of the cell there is a small vacuole containing minute crystals of gypsum in constant motion. Many Desmids are characterised by heliotactic movements ; they protrude fine mucilaginous threads through the cell walls, by means of which they can push themselves along, and take up a position in a line with the direction of the incident rays of light.

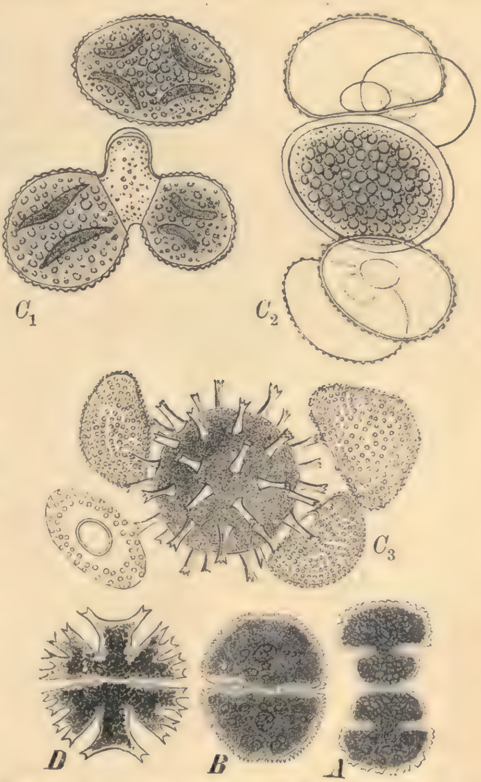


Fig. 271.—*A*, *Cosmarium coelatum*, dividing. *B*, *C*, *Cosmarium botrytis*. C_1, two cells at right angles preparing for conjugation—the lower cell shows the conjugation canal : C_2, gametes fused into the young zygote ; C_3, mature zygote ; *D*, *Micrasterias crux melitensis*. (After Ralfs : C_1, C_2, after De Bary.)

Multiplication is effected by cell-division. This is accomplished by the formation of a partition wall across the middle of the cell after the nuclear division is completed. Each daughter cell eventually attains the size and form of the mother cell, by the outgrowth of a new half on the side towards the new division wall (Fig. 271 *A*).

The conjugation of the protoplasts takes place, in the case of the Desmidiaceae, outside their cell-walls. Two cells approach each other, and surround themselves with a mucilaginous envelope. Their cell-walls rupture at the constriction, and parting in half allow the protoplasts to escape; these then unite to form a zygospore. The zygospores frequently present a very characteristic appearance, as their walls are often beset with spines (Fig. 271 *C*). The four empty cell halves may be seen close to the spore. In some Desmidiaceae the conjugating cells undergo a preliminary division, the daughter cells uniting in pairs.

The two sexual nuclei in the zygote do not fuse until germination of the latter is about to commence. The resulting nucleus then undergoes division into four nuclei, two large and two small. Only two cells are formed from the zygote each of which has thus two nuclei of different sizes; the smaller nuclei disappear. The production of two cells on germination thus appears to be derived from the division into four cells seen in *Mesotaenium*, and to stand to the latter as a reduced form.

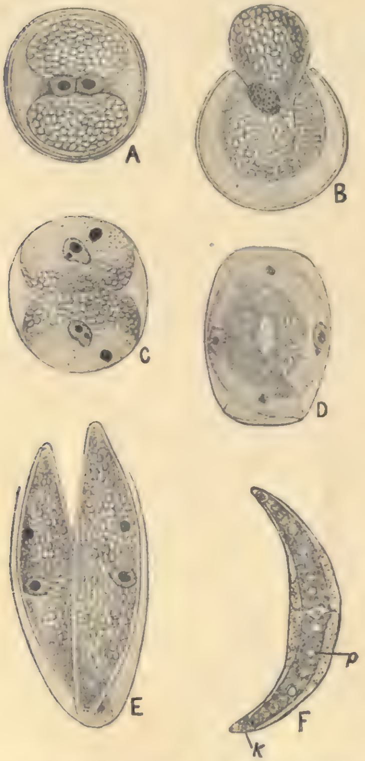


FIG. 272.—*Closterium*. *A*, Zygote before germination showing the two nuclei not yet united; *B*, germinating zygote with the nuclei united; *C*, division into two cells each containing one larger and one smaller nucleus; *D*, further state of germination; *E*, young plants escaping from the cell-membrane; *F*, *Closterium moniliforme*, mature plant. (*A-E* after KLEBAHN.)

3. **Zygnemaceae.**—In this family, all of which are filamentous in character, the genus *Spirogyra*, with its numerous species, is the best known. It is commonly found in standing water, forming unattached masses of tangled green filaments. The filaments exhibit no distinction of base and apex, and are composed of simple rows of cells, which vary in length in different species. Growth results from the division and elongation of the cells in one direction only. Each cell has a large nucleus and one or several spiral green band-like chromatophores (Fig. 273 *C*), The cells of *Zygnema* contain two star-shaped chromatophores.

CONJUGATION, in the case of *Spirogyra*, is preceded by the development of converging lateral processes from the cells of adjacent filaments. When two processes from opposite cells meet (Fig. 273 *A*), their walls become absorbed at the point of contact, and the whole protoplasmic contents of one cell, after contracting from the cell wall, passes through the canal which is thus formed into the opposite cell. The protoplasm and nuclei of the conjugating protoplasts then fuse together while the chloroplasts do not unite, but those of the entering protoplast disorganise. The resulting cell forms the zygospore invested with a thick wall, and filled with fatty substances and reddish-brown mucilage-spheres. This form of conjugation, which is the one exhibited by most species, is described as scalariform (Fig. 273 *A*), as distinct from the lateral conjugation of some species, in which two adjacent cells of the same filament conjugate by the development of coalescing processes, which are formed near their transverse wall (Fig. 273 *B*). In some genera the zygote is formed midway in the conjugation tube.

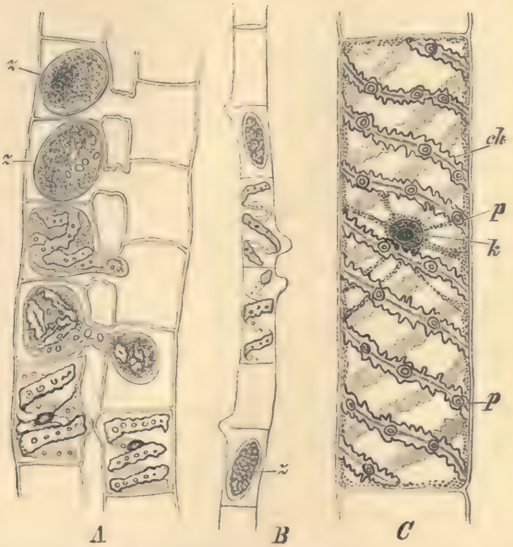


FIG. 273.—*A*, Conjugation of *Spirogyra quinina* (× 240). *B*, *Spirogyra longata* (× 150); *z*, zygospore. *C*, Cell of *Spirogyra jugalis*; *k*, nucleus; *ch*, chromatophores; *p*, pyrenoid. (× 256.)

On germination the zygote gives rise to only one plant; its contents grow out as a cylindrical cell which on division forms a filament. According to CHIMIELEWSKY the nucleus of the zygote of Spirogyra first divides amitotically into four, two of which disintegrate while the remaining two again fuse to form the single nucleus of the young plant ([16]).

CLASS VII

Diatomeae (Diatoms) ([6, 17])

The Diatomeae (Bacillariaceae) constitute a very large class of unicellular Algae. They occur usually associated together in large numbers, in both fresh and salt water, and also on damp soil.

The cells are either solitary or form colonies; they are free-swimming, or are attached by means of gelatinous stalks, excreted by the cells themselves (Fig. 274). Sometimes the cells remain connected and form bands or zigzag chains, or, on the other hand, they are attached and enclosed in gelatinous tubes, while in the case of the marine genus *Schizonema* they lie embedded in large numbers in a gelatinous branching thallus, often over 1 dcm. in size. The cells also display a great diversity of shape; while generally bilaterally symmetrical, they may be circular or elliptical, rod- or wedge-shaped, curved or straight. The structure of their cell walls is especially characteristic; it is composed of two halves or VALVES, one of which overlaps the other like the lid of a box (Fig. 3, *B*). The cells thus present two altogether different views, according to the position in which they are observed, whether from the GIRDLE (Fig. 3 *B*) or VALVE SIDE (Fig. 3 *A*). The two valves are so strongly impregnated with silica, that, even when subjected to intense heat, they remain as a siliceous skeleton, retaining the original form and markings of the cell walls. The walls of the cells, particularly on the valve side, are often ornamented with numerous fine, transverse

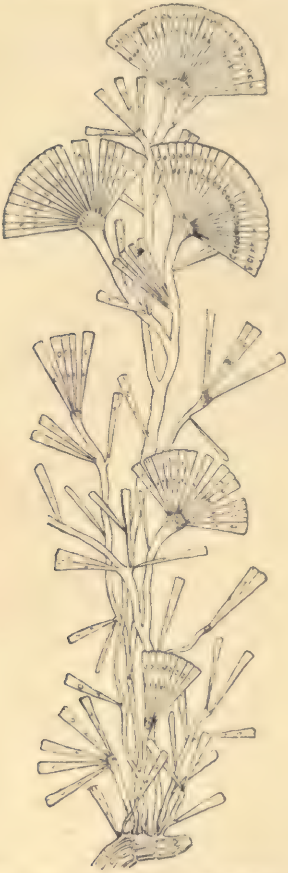


FIG. 274.—*Licmophora flabellata.* Colony of Diatoms with branched gelatinous stalks. (After SMITH, from GOEBEL'S *Organographie.*)

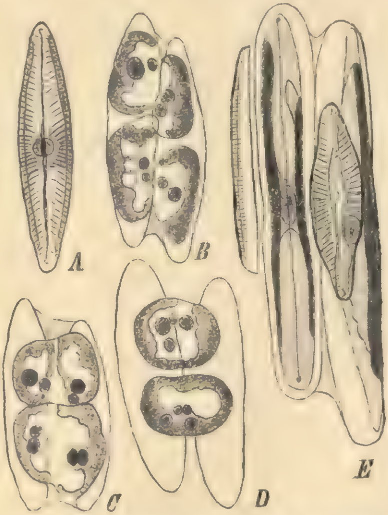


FIG. 275.—Formation of auxospores in *Navicula viridula.* *A*, Cell seen from the valve side. *B*, Two cells lying alongside one another; their contents have divided into two daughter cells, each of which possesses two nuclei. *C*, *D*, Conjugation in pairs of the daughter cells to form the auxospores, which at first contain four nuclei. *E*, The two full-grown auxospores; the two larger nuclei in each have fused into one, the two smaller ones have disintegrated. (After KARSTEN. × 500.)

markings or ribs, and also with small protuberances and pits, or they are perforated by open pores which serve to give exit to the gelatinous secretion and possibly play a part in the movements sometimes exhibited by the cells.

According to the structure of the cell walls two main groups of Diatoms are distinguished, the Centricae (Fig. 277) with usually circular valves and radial or concentric sculpturing, and the Pennatae the valves of which are usually elongated and the sculpturing pinnate. In many of the Pennatae (Fig. 3) a longitudinal line corresponding to an opening in the cell walls, and exhibiting swollen nodules at both extremities and in the middle, is distinguishable in the surface of the valves. Forms provided with such a median suture or RAPHE are characterised by peculiar backward-creeping movements, resulting from the extrusion of protoplasmic protrusions from the spirally arranged longitudinal slits which are present in the raphe (cf. p. 266).

The cell has always a central nucleus and one (Fig. 3) or two to four (Fig. 275) large or numerous smaller chromatophores (Fig. 277) embedded in its parietal protoplasm. These chromatophores are flat, frequently lobed, and of a brownish-yellow colour. Globules of a fatty oil are also included in the cell contents, and take the place of starch as an assimilation product.

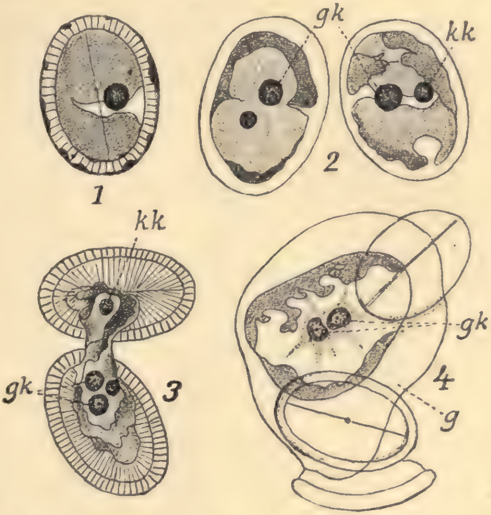


FIG. 276.—*Cocconeïs placentula.* *1*, Vegetative cell; *2*, pair of cells before conjugation; *3*, *4*, cells in process of conjugation. *gk*, Large nucleus; *kk*, small nucleus; *g*, gelatinous substance. (After KARSTEN, from OLTMANNS' *Algae*.)

The Diatomeae multiply vegetatively by longitudinal division which always takes place in one direction. In this process the two valves are first pushed apart from one another by the increasing protoplasmic contents of the mother cell, which then divides longitudinally in such a direction that each of the two new cells retains one valve of the mother cell. After the division of the protoplasm of the mother cell is accomplished, each daughter cell forms, on its naked side, a new valve fitting into the old one. The two valves of a cell are therefore of different ages. In consequence of this peculiar manner of division, as the walls of the cells are silicified and incapable of distension, the daughter cells become successively smaller and smaller, until finally, after becoming reduced to a definite minimum size, they undergo transformation into AUXOSPORES. The auxospores are usually two or three times larger than the cells from which they arise, and by their further development they re-establish the original size of the cells.

The formation of the auxospores, which correspond to the zygospores of the Conjugatae, is accomplished in various ways. The process in *Navicula* (Fig. 275), *Pleurosigma*, etc., may be compared with the zygospore formation of *Spirotaenia*; two cells lay themselves side by side, the protoplast of each undergoes division into two, and the resulting cells emerge from the valves of the cell wall and conjugate in pairs. By division of the nucleus each gamete was provided with a larger and a smaller nucleus; in the auxospores the two large nuclei fuse, while the two small nuclei disintegrate.

In *Surirella* and *Cocconeis* (Fig. 276) the conjugating cells do not undergo division, but unite directly with one another. The nuclei, however, divide; in the former genus two nuclear divisions occur in each of the conjugating cells, resulting in one large and three small nuclei; in the latter genus there is only a single nuclear division giving one large and one small nucleus. The large nuclei fuse, the small ones degenerate.

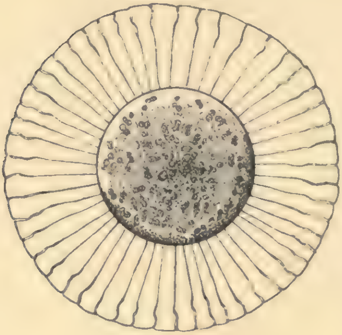


FIG. 277. — *Planktoniella sol.* A disc-shaped Diatom from the Plankton. A parachute-like, hollow membranous wing springs from the girdle. (After SCHÜTT. × 190.)

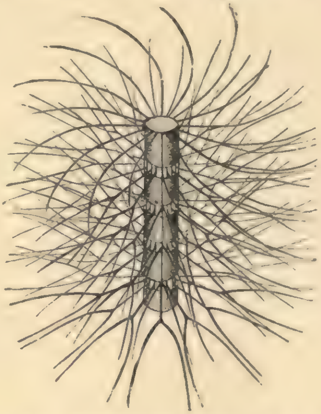


FIG. 278.—*Bacteriastrum varians.* From the Plankton. A chain of cells which bear bristles as a floating apparatus. (After SCHÜTT. × 200.)

In *Achnanthes* the cell contents of a single cell divides into two daughter cells, which escape, and then fuse together to form the auxospore.

In many genera sexuality is not obvious in the process of forming the auxospores, which arise asexually from cells that do not conjugate. This is the case in *Synedra* and *Rhabdonema*, in which a cell divides and the two daughter cells emerge and develop into auxospores. In *Melosira* there is no longer any cell division, the protoplast enlarges, bursts the cell wall, and becomes directly transformed into an auxospore. The original preliminary divisions are, however, still frequently indicated by nuclear divisions, in *Melosira* only by the appearance of two nucleoli in the nucleus of the auxospore.

Some plankton Diatoms exhibit a breaking up of the protoplast by repeated cell division into numerous small, round, naked daughter cells. According to KARSTEN's observations in *Corethron*, these cells escape, conjugate in pairs, the resulting zygotes increase in size, and on germination give rise to two daughter cells. Each of the latter has at first two nuclei, one of which later disappears, and the cell grows into a mature individual of *Corethron*. These processes call to mind the behaviour of *Closterium* among the Desmidiaceae (18).

Countless numbers of Diatoms live in the ocean, and they constitute also a proportionately large part of the PLANKTON (12), that is, the free-swimming organic world on the surface of the sea. The plankton Diatoms are mostly centric forms, have no middle suture or raphe on the surface of their valves, and are especially adapted to swimming or floating. To this end they are often provided with horn-like protuberances or membranous wings, which greatly enhance their buoyancy (Figs. 277, 278).

Many Diatoms occur in places where decomposing substances are present in abundance. Such species can assume a saprophytic mode of life, their chromatophores becoming colourless and reduced in size. It has been shown that some colourless species of *Nitzschia* which occur in the sea are exclusively dependent on organic substances for food, the reduction of their chromatophores being complete (19).

Diatoms occur also as fossils. Their silicified valves form a large part of the deposits of SILICEOUS EARTH (Kieselguhr, mountain meal, etc.,) and in this form they are utilised in the manufacture of dynamite.

On account of the extreme fineness of the markings of their valves, it is customary to employ certain species of Diatoms as test objects for trying the lenses of microscopes. *Pleurosigma angulatum* is commonly used for this purpose.

CLASS VIII

Heterocontae (6)

In the Heterocontae a number of genera of green Algae are included which were formerly placed in the Chlorophyceae but are now separated as an independent class.

At the base of the class may be placed such true Flagellata as *Chloramoeba heteromorpha* (Fig. 279), which lives in fresh water. The naked, amœboid cell contains a nucleus and 2-6 yellowish-green chloroplasts; at the anterior end, just outside a vacuole, two cilia are situated which are of very unequal length. It is this last feature which gives the name to the group. *Chloramoeba* is one of those low green organisms which become colourless and lose the power of independent nutrition when cultivated in a nutritive solution in the dark. Thick-walled resting cells also occur.

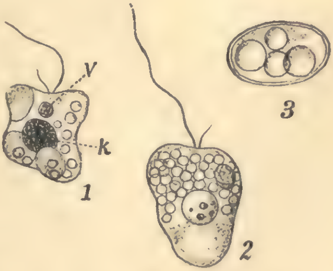


FIG. 279. — *Chloramoeba heteromorpha*: *v*, vacuole; *k*, nucleus; *3*, a resting cell. (After BOHLIN, from OLTMANNS' *Algae*.)

Among the higher Heterocontae characterised by the presence of pectin in the cell wall the genus *Conferva* which is widely spread in fresh water must be mentioned (Fig. 280). The plant consists of simple unbranched filaments the cells of which have peculiarly constructed walls; the wall consists of two parts separated by an oblique annular split at the middle part of the cell. On cell division a new portion, H-shaped in longitudinal section, is intercalated. The characteristics of the group are seen in the yellowish-green, oil-forming chloroplasts, and the formation of zoospores with cilia of unequal lengths (in many Confervae the zoospores have only a single cilium). In addition to zoospores thick-walled aplanospores arise by the separation by the cells of the filament.

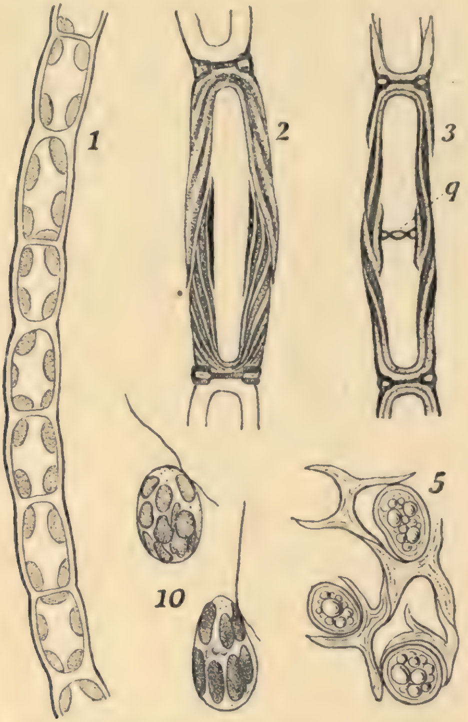


FIG. 280.—*Conferva bombycina.* *1*, Filament; *2*, *3*, formation of transverse wall (*q*) in cell division; *5*, formation of aplanospores by breaking down of the filament; *10*, Zoospores with cilia of unequal length. (After GAY (*1*, *5*), BOHLIN (*2*, *3*), LUTHER (*10*). From OLTMANNS' *Algae.*)

With some reservation OLTMANNS also places here *Botrydium granulatum* (Fig. 281), which was formerly included in the *Siphoneae*. This Alga grows on damp clayey soil, where it forms groups of green, balloon-shaped vesicles about 2 mm. in breadth. These are attached to the soil by branched colourless rhizoids. The whole plant corresponds to a single multinucleate cell; its protoplasm contains numerous green chloroplasts. The zoospores, produced in large numbers by the division up of the contents, escape by an opening at the summit. Each has a single cilium and contains two chloroplasts. After swarming the spore surrounds itself with a wall and grows into one of the balloon-shaped plants ([1]).

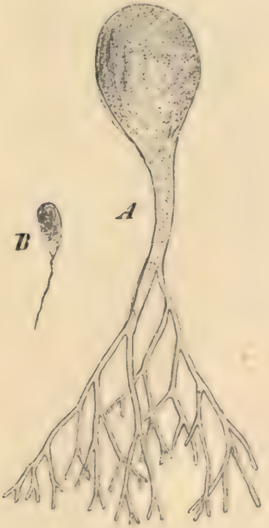


FIG. 281.—*A*, *B*, *Botrydium granulatum.* *A*, The whole plant; *B*, Swarm-spore. (*A* × 28; *B* × 540.)

In some genera, gametes resembling the zoospores but conjugating in pairs have been observed.

CLASS IX

Chlorophyceae (6, 20, 21)

When the green Conjugatae and Heterocontae are separated there remains the natural group of the Chlorophyceae, including several series of genera. The majority of these Algae live in fresh water or in damp situations, but a large number are found in the sea. Their characteristic chloroplasts are of a pure green colour, frequently contain pyrenoids, and nearly always form starch. The asexual swarm-spores are pear-shaped, and in typical forms possess two or four cilia of equal length (on this account the group is sometimes termed Isocontae) and a curved or bowl-shaped chloroplast. In some genera the swarm-spores are replaced by non-motile aplanospores, and in certain of the more advanced genera (*Oedogonium*, *Vaucheria*) the swarm-spores are of more complicated structure, but can be derived from the typical simple form.

Of the five orders included in the Chlorophyceae the Volvocales stands nearest to the Flagellata and, as is also the case with the Protococcales, include unicellular and colonial forms. The Ulotrichales and Siphonocladiales are filamentous; in the former the filaments are composed of uninucleate, in the latter of large multinucleate cells. The filaments are simple in the lower forms, but branched in the more advanced ones. The thallus of the Siphonales is formed of a single multinucleate cell.

In all the orders sexual reproduction is usually effected by the conjugation of gametes which resemble the zoospores. In all the groups, except the Protococcales, isogamy is replaced by oogamy in the higher forms.

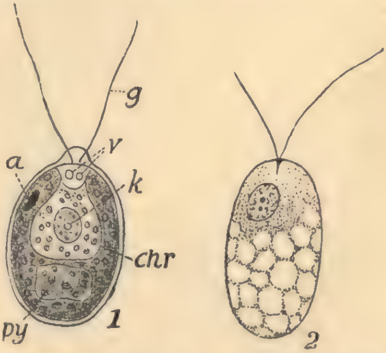


FIG. 282.—*1. Chlamydomonas angulosa.* (After DILL.) *g*, cilia; *v*, vacuole; *k*, nucleus; *chr*, chromatophores; *py*, pyrenoid. *2. Polytoma uvella* (after DANGEARD); *a*, eye-spot. (From OLTMANNS' *Algae*.)

Order 1. Volvocales.—Typical representatives of this order are characterised by the cilia being retained by their cells in the vegetative stage; the plants are therefore motile. Each cell has a nucleus and a chloroplast. The Volvocales thus resemble the Flagellata, some forms of which, such as *Polyblepharis*, might, on the ground of their cell structure, be placed in the former group, but differ by the absence of a cell wall and of sexual reproduction.

Chlamydomonas (Fig. 282) and *Haematococcus* (Fig. 283) are widely distributed forms consisting of free-swimming cells (22). In the former the cell membrane is closely applied to the protoplast, at the anterior end of which two cilia and a red eye-spot are situated ; in the latter genus the membrane is separated from

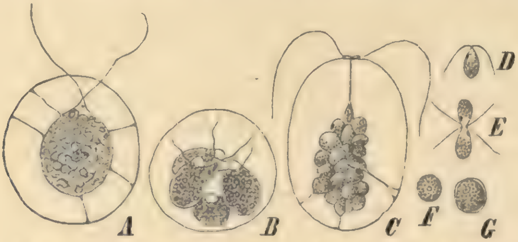


FIG. 283.—*A*, *B*, *Haematococcus plurialis* (× 360) ; *A*, swarming cell ; *B*, formation of swarm-spores. *C-G*, *Haematococcus Bütschlii* ; *C*, formation of gametes (× 400) ; *D*, gamete ; *E*, conjugation of two gametes ; *F*, *G*, zygotes (× 800). (*C-G*, after BLOCHMANN.)

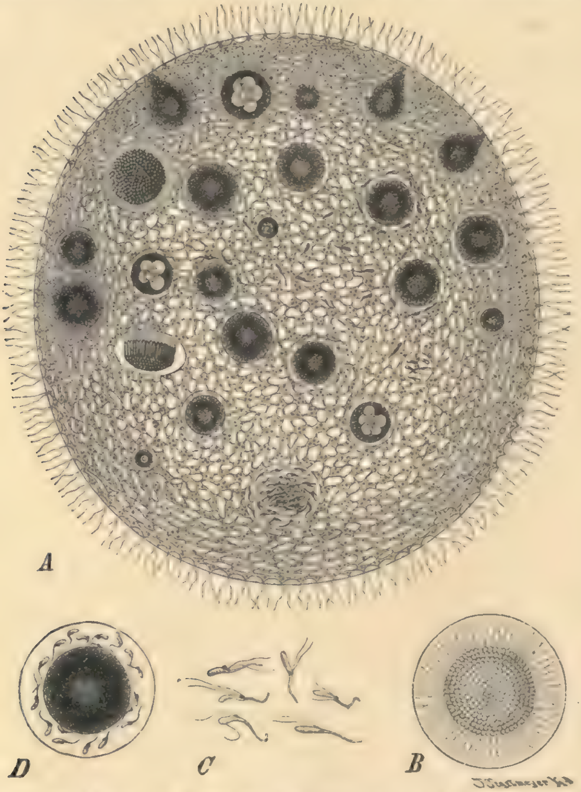


FIG. 284.—*Volvox globator*. *A*, Colony showing various stages of development of ova and spermatozoids (× 165). *B*, Bundle of spermatozoids formed by division from a single cell (× 530). *C*, Spermatozoids (× 530). *D*, Egg-cell surrounded by spermatozoids in the mucilaginous membrane (× 265). (After F. COHN.)

the protoplast by a gelatinous layer except at the anterior end. *Haematococcus pluvialis* occurs commonly in puddles of rain-water, and, like *Chlamydomonas nivalis*, which gives rise to "red snow" and occurs on snow in the Alps, etc., is characterised by the presence of a red pigment (haematochrome) in the cells. Reproduction is both asexual, by swarm-spores, 2-8-16 of which are formed in a mother cell and are set free by rupture of the membrane, and sexual; the sexual reproduction is by conjugation of similar, small, biciliate gametes formed in large numbers (to 64) in a mother cell, and uniting in pairs by their anterior ends to form a zygote. In *Chlamydomonas coccifera*, according to GOROSCHANKIN (23), there is in contrast to the other species a marked differentiation in the sexual cells. Single cells become transformed into large, non-ciliated, female gametes or egg-cells; others divide and each gives rise to 16 small, biciliate male gametes. The transition to oogamy thus occurs in this group even among the isolated unicellular forms.

Polytoma uvella, which resembles *Chlamydomonas* in structure, is a colourless and saprophytic form (Fig. 282, 2).

The biciliate cells of *Pandorina*, *Eudorina*, *Volvox*, etc., are united in colonies or coenobia. In *Volvox* (24) (Fig. 284), which may be regarded as the highest form in the order, the free-swimming colonies have the shape of a hollow sphere. The component protoplasts are connected by fine processes, so that the organism must be regarded as constituting a single individual. The sexual cells are differentiated into ova and spermatozoids. The egg-cells arise by the enlargement of single cells of the colony; they are large, green, non-motile cells surrounded by a mucilaginous wall. The small spermatozoids are elongated bodies of a bright yellow colour, provided with two cilia at the colourless anterior end; they arise by the division of a cell of the colony into numerous daughter cells. After fusing with a spermatozoid within the cavity of the colony the egg-cell is transformed into the thick-walled, resting oospore. The vegetative reproduction of *Volvox* takes place by the division of single cells of the colony to form a new daughter colony; this corresponds to the formation of swarm-spores in other genera. *Eudorina* is also oogamous.

Order 2. Protococcales.—These are unicellular green Algæ, or their cells are united in colonies of various form; the vegetative cells have no cilia, and the cell or colony is consequently non-motile. Usually each cell contains a nucleus and only one chloroplast. Reproduction is by means of zoospores, in place of which in many genera non-ciliated aplanospores are found. Sexual reproduction, when present, takes the form of conjugation of similar gametes.

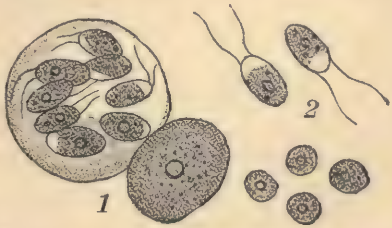


FIG. 285.—*Chlorococcum* (*Chlorosphaera*) *limicola*. *1*, Vegetative cell and cell divided into 8 zoospores; *2*, free zoospores; *3*, zoospores after they have formed cell-walls. (After BEYERINCK, from OLTMANNS' *Algae*.)

The simplest forms belong to the genera *Chlorococcum* (including *Cystococcus*) and *Chlorella* (25, 26). The cells of the former are spherical, and occur in fresh water and also on damp substrata; they frequently take part in the composition of Lichen thalli. Asexual reproduction is by the production from a cell of a number of biciliate zoospores (Fig. 285); under certain conditions these are replaced by aplanospores without cilia. *Chlorella vulgaris* (Fig. 286) is a wide-spread Alga, the small cells of which often live symbiotically in the protoplasts of lower animals (Infusoriae, *Hydra*, *Spongilla*, Planariae); it is multiplied only by division of the cells into 2, 4, or 8 aplanospores which surround themselves with a wall and grow to the full size.

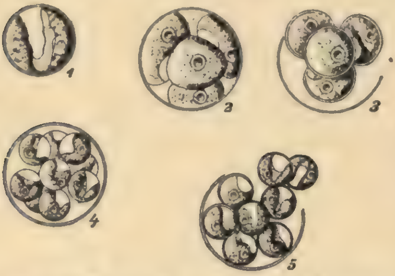


FIG. 286.—*Chlorella vulgaris*. *1*, Cell; *2*, *3*, division into four aplanospores; *4*, *5*, division into eight aplanospores. (After GRINTZESCO.)

The simplest type of cell-colony, consisting of four cells, is found in the genus *Scenedesmus* (27), which is widely spread in fresh water, and connects on to *Chlorella*. The commonest form, *Sc. acutus*, has spindle-shaped cells, while the colonies of *Sc. caudatus* are distinguished by four long horn-like prolongations of the cell wall (Fig. 287). In reproduction each cell divides in the direction of its length into four daughter-cells, which, on escaping from the parent cell form a new colony. More complicated cell colonies are met with in *Pediastrum* (28) (Fig. 288), in which each cell-family forms a free-swimming plate, composed internally of polygonal cells, while on the margin it consists of cells more or less acutely crenated. The formation of asexual swarm-spores is effected in *Pediastrum* by the division of the contents of a cell into a number (in the case of the species illustrated, *P. granulatum*, into 16) of naked **swarm-spores, each with two cilia. The swarm-spores, on escaping through the ruptured cell wall (Fig. *A*, *b*), are enclosed in a common envelope. After first moving vigorously about within this envelope, they eventually collect together and form** a new cell-family. *Pediastrum* also possesses a sexual mode of reproduction. The gametes are all of equal size, and except that they are smaller and are produced in greater numbers, are similar to the swarm-spores. They move freely about in the water, and in conjugating fuse in pairs to form zygotes. The further development of the zygotes into cell-families is not yet fully known.

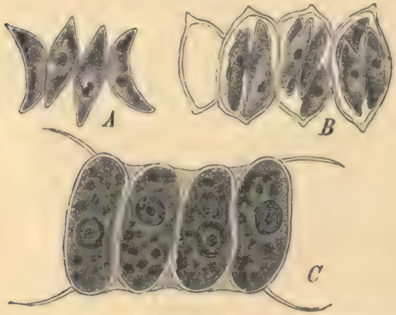


FIG. 287.—*A*, *Scenedesmus acutus*. *B*, the same, undergoing division; *C*, *Scenedesmus caudatus*. (After SENN, × 1000.)

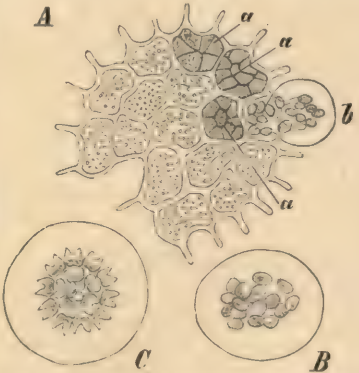


FIG. 288.—*Pediastrum granulatum*. *A*, An old cell-family: *a*, cells containing spores; *b*, spores in process of extrusion (the other cells have already discharged their spores); *B*, cell-family shortly after extrusion of the spores; *C*, cell-family 4½ hours later. (After AL. BRAUN, × 300.)

The life-history of the Water-net (*Hydrodictyon utriculatum* (1, 29) is essentially similar. It is one of the most beautiful of the free-floating, fresh-water Algae, the hollow cylindrical colonies being formed of elongated cells united together to form a many-meshed net.

Order 3. Ulotrichales.—The Ulotrichales exhibit, as compared with the unicellular green Algae, an advance in the external segmentation of the thallus. It is always multicellular, and, in most of the genera, consists of simple or branched filaments. The filaments are either attached by a colourless basal cell to the substratum (Fig. 290 *A*) or float free. The thallus of the marine genus *Ulva* (*Ulva lactuca*, SEA LETTUCE) has the form of a large, leaf-like cell surface, and is two layers of cells thick (Fig. 5, p. 13). In *Enteromorpha* (Fig. 289) the thallus is ribbon-shaped, either cylindrical or flattened; when young it is two-layered, but later it becomes hollow, the wall thus consisting of one layer of cells. Although the majority of the Ulotrichales live in fresh or salt water, a few aerial forms (Chroolepideae) grow on stones, trunks of trees, and, in the tropics, on leaves. To this family belongs *Trentepohlia* (or *Chroolepus*) *Jolithus*, often found growing on stones in mountainous regions. The cell filaments of this species appear red on account of the hæmatochrome they contain, and possess a violet-like odour.

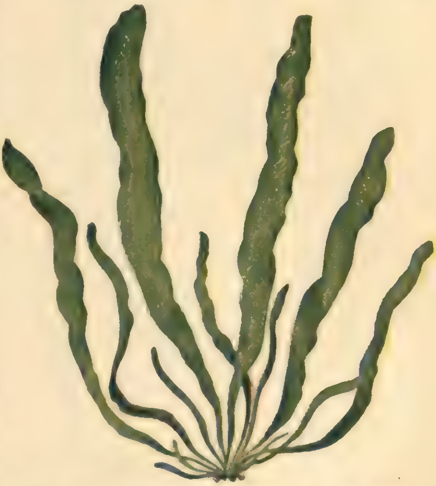


FIG. 289.—*Enteromorpha compressa*. (½ nat. size.)

The asexual reproduction is accomplished by the formation of ciliated swarm-spores. Sexual reproduction is effected either by the fusion of planogametes, or the sexual cells are differentiated as non-motile egg-cells and motile spermatozoids.

Ulothrix zonata (30) (Fig. 290 *A*) is one of the commonest filamentous Algae. The filaments of *Ulothrix* exhibit no pronounced apical growth; they are unbranched, attached by a rhizoid cell, and consist of single rows of short cells; each cell contains a band-shaped chloroplast. The asexual reproduction is effected by means of swarm-spores, which have four cilia (*C*), and are formed by division in any cell of the filament. The swarm-spores escape through a lateral opening (*B*) formed by absorption of the cell wall, and, after swarming, give rise to new filaments. The sexual swarm-cells, or planogametes, are formed in a similar manner by the division of the cells, but in much greater numbers. They are also smaller, and possess only two cilia (*E*). In other respects they resemble the swarm-spores, and possess a red eye-spot and one chromatophore. By the conjugation of the planogametes in pairs, zygotes (*F*-*H*) are produced, which, after drawing in their cilia, round themselves off and become invested with a cell wall. After a shorter or longer period of rest the zygotes are converted into unicellular germ plants (*J*), and give rise to several swarm-spores (*K*), which in turn grow out into new filaments. Under some conditions the planogametes can give rise to new plants parthenogenetically without conjugating. Further, the filaments can, in addition to the swarm-spores with four cilia described above, produce others of smaller size (micro-zoospores) which resemble the gametes. These possess four or two cilia, and as a rule die if the temperature of the medium is above 10° ; below this temperature they come to rest after a few days and proceed to germinate slowly. This Alga is thus of interest from the incomplete sexual differentiation exhibited by its gametes.

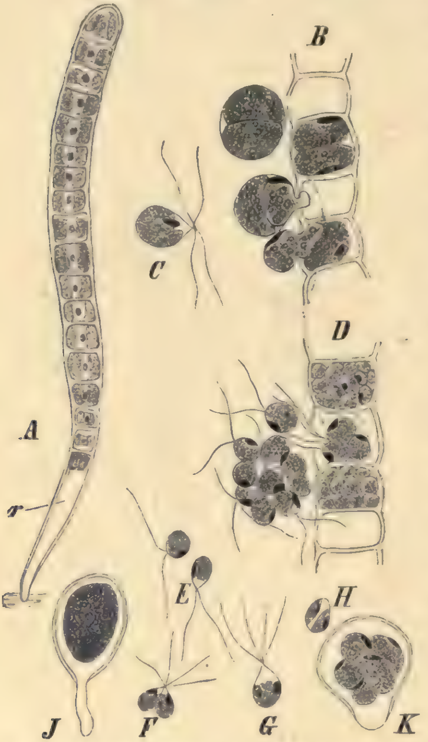


FIG. 290.—*Ulothrix zonata.* *A*, Young filament with rhizoid cell *r* (× 300) ; *B*, portion of filament with escaping swarm-spores ; *C*, single swarm-spore ; *D*, formation and escape of gametes ; *E*, gametes ; *F*, *G*, conjugation of two gametes ; *H*, zygote ; *J*, zygote after period of rest ; *K*, zygote after division into swarm-spores. (After DODEL-PORT. *B*-*K* × 482.)

The genera *Oedogonium* ([31]) and *Bulbochaete* may be quoted as examples of oogamous Ulotrichales. While the thallus of the latter is branched, the numerous species of *Oedogonium* consist of unbranched filaments, each cell of which possesses one nucleus and a single parietal chromatophore composed of numerous united bands. The asexual swarm-spores of Oedogonium are unusually large, and have a circlet of cilia around their kinoplasmic, colourless, anterior extremity (Fig. 291 *B*). In this case the swarm-spores are formed singly, from the whole contents of any single cell of the filament (*A*), and escape by the rupture of the cell wall. After becoming attached by the colourless end they germinate, giving rise to a new filament. For the purpose of sexual reproduction, on the other hand, special cells become swollen and differentiated into barrel-shaped oogonia. A single large egg-cell with a colourless receptive spot is formed in each oogonium by the contraction of its protoplasm, while the wall of the oogonium becomes perforated by an opening at a point opposite the receptive spot of the egg. At the same time, other, generally shorter, cells of the same or another filament become converted into antheridia. Each antheridium usually gives rise to two spermatozoids. The spermatozoids are smaller than the asexual swarm-spores, but have a similar circlet of cilia. They penetrate the opening in the oogonium and fuse with the egg cell, which then becomes transformed into a large, firm-walled oospore. On the germination of the oospore its contents become divided into four swarm-spores, each of which gives rise to a new cell filament. In the adjoining figure (Fig. 292) a germinating oospore of *Bulbochaete* with four swarm-spores is represented.

In some species of *Oedogonium* the process of sexual reproduction is more complicated, and the spermatozoids are produced in so-called DWARF MALES. These are short filaments (Fig. 291 *C*, *a*) consisting of but few cells, and are developed from asexual swarm-spores (ANDROSPORES) which, after swarming, attach themselves to the female filaments, or even to the oogonia. In the upper cells of the dwarf male filaments thus derived from the androspores, spermatozoids are produced which are set free by the opening of a cap-like lid (Fig. 291 *D*, *a*).

The genus *Coleochaete* ([32]) is also oogamous. The long colourless neck of the flask-shaped oogonium opens at the tip to allow of the entrance of the spermatozoid. The spherical oospore increases in size and becomes surrounded by a single layer of pseudo-parenchymatous tissue derived from filaments that spring from the stalk cell of the oogonium and neighbouring cells. In this way a fruit-like body is formed. On germination the oospore first divides into 16-32 wedge-shaped cells, then breaks up and liberates a swarm-spore from each cell. While in regard to these processes *Coleochaete* exhibits the highest grade attained by the Green Algae, it cannot be regarded as the point of origin of the Bryophyta.

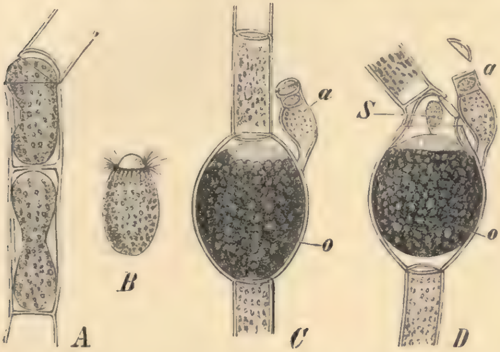


FIG. 291.—*A*, *B*. *Oedogonium* : *A*, escaping swarm-spores ; *B*, free swarm-spore. *C*, *D*, *Oedogonium ciliatum* : *C*, before fertilisation ; *D*, in process of fertilisation ; *o*, oogonia ; *a*, dwarf males ; *S*, spermatozoid. (After PRINGSHEIM, × 350.)

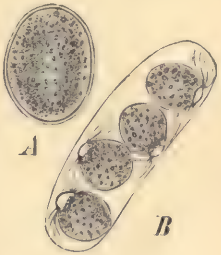


FIG. 292. *Bulbochaete intermedia*. *A*, Oospore ; *B*, formation of four swarm-spores in the germinating oospore. (After PRINGSHEIM, × 250.)

Order 4. Siphonocladiales.—The Algae of this order are filamentous and usually branched ; they are distinguished from the Ulotrichales by their large multinucleate cells, the chloroplasts of which are either solitary, large and reticulately formed, or appear as numerous small discs.

The genus *Cladophora*, numerous species of which occur in the sea and in fresh water, is one of the most important representatives of the order. *Cl. glomerata* (Fig. 293) is one of the commonest Algae in streams, often attaining the length of a foot. It is attached by rhizoid-like cells, and consists of branched filaments with typical apical growth which some other representatives of the order do not show. The structure of the cells is represented in Fig. 61. Branching takes place from the upper ends of the cells by the formation of a protrusion which is cut off as the first cell of the branch. Asexual reproduction is by means of biciliate zoospores (Fig. 293), which arise in numbers from the upper cells of the filaments, and escape from these sporangia by a lateral opening in the wall. The sexual reproduction is isogamous as in *Ulothrix*.

Only in the genus *Sphaeroplea* has the sexual reproduction become oogamous. *S. annulina* consists of simple filaments and occurs in fresh water.

Many forms occur in the sea (*e.g.* *Siphonocladus*), and some have a highly complicated thallus, which is always, however, formed of branched filaments ; by calcareous incrustation some forms come to resemble coral. *Acetabularia mediterranea* (33) (Fig. 294) will serve as an example of such calcareous Algae. The thin stalk of the thallus is attached by means of rhizoids, while the umbrella-like disc consists of closely united tubular outgrowths, each of which is to be regarded as a gametangium. The contents of the latter do not form the biciliate gametes directly, but first divide into a large number of firm-walled cysts. These remain in the resting condition throughout the winter, and then give rise to numerous gametes which conjugate in pairs. The zygotes germinate promptly and grow into new plants.

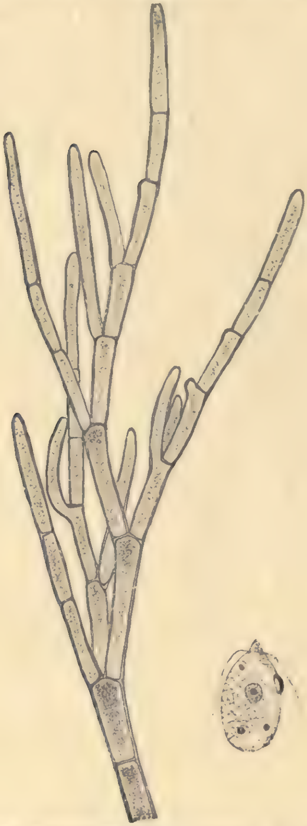


FIG. 293.—Portion of *Cladophora glomerata*. (× 48.) To the right a swarm-spore. (× 1000.)

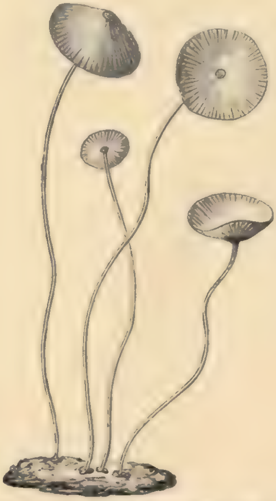


FIG. 294.—*Acetabularia mediterranea*. (Nat. size.)

Order 5. Siphonales.—The Siphoneae are distinguished from the preceding groups of Algae by the structure of their thallus, which, although more or less profusely branched, is not at first divided by transverse septa. The cell-wall thus encloses a continuous protoplasmic body in which numerous nuclei and small green chloroplasts are embedded. The same type of thallus is also met with in the Phycomycetes or Algal Fungi.

The majority of the Siphoneae inhabit the sea, and on account of the complicated segmentation of their thallus, afford one of the most interesting types of algal development. The genus *Caulerpa* (34), represented by many species inhabiting the warmer water of the ocean, has a creeping main axis. Increasing in length by apical growth, the stem-like portion of the thallus gives off from its under surface profusely branched colourless rhizoids, while, from its upper side, it produces green thalloid segments which vary in shape in the different species. In *Caulerpa prolifera* (Fig. 295) these outgrowths are leaf-like and are frequently proliferous. In other species they are pinnately lobed or branched. The whole thallus, however branched and segmented it may be, encloses but one cell-cavity, which is, however, often traversed by a network of cross-supports or trabeculæ. Starch-forming leucoplasts are present in the colourless parts of the thallus.

The genus *Bryopsis*, on the other hand, has a delicate, pinnately branched thallus. The thallus of *Halimeda*, the species of which occur in the warmer seas, is composed of flattened segments, and resembles an *Opuntia* on a small scale. By incrustation with lime it attains a hard, coral-like texture. The segments are formed of branched tubular filaments.

In *Bryopsis* the conjugating gametes are differentiated into a larger female cell and a smaller male cell; in *Vaucheria* and *Dichotomosiphon* oogamous reproduction is well marked (35). The latter Algae occur in fresh water or on damp soil. The thallus consists of a single branched, filamentous cell attached to the substratum by means of colourless rhizoids (Fig. 296 *D*).

The swarm-spores of *Vaucheria*, which differ from those of the other Siphonales, are developed in special sporangia, cut off from the swollen extremities of lateral branches by means of transverse walls (Fig. 296). The whole contents of such a sporangium become converted into a single, green swarm-spore. The wall of the sporangium then ruptures at the apex, and the swarm-spore, rotating on its longitudinal axis, forces its way through the opening. The swarm-spore is so large as to be visible to the naked eye, and contains numerous nuclei embedded in a peripheral layer of colourless protoplasm. It is entirely surrounded with a fringe of cilia, which protrude in pairs, one pair opposite each nucleus. Morphologically the swarm-spores of *Vaucheria* correspond to the collective, individual zoospores of an ordinary sporangium.

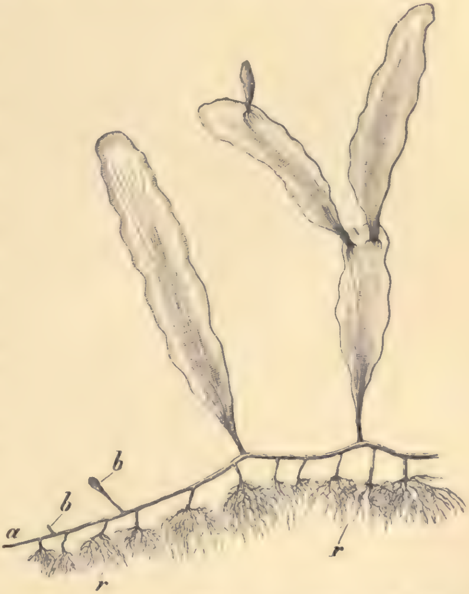


FIG. 295.—*Caulerpa prolifera*. The shaded lines on the thallus leaves indicate the currents of protoplasmic movement; *a*, growing apex of the thallus axis; *b*, *b*, young thallus lobes; *r*, rhizoids. (½ nat. size.)

The sexual reproduction of *Vaucheria* is not effected, like that of the other Siphoneae, by the conjugation of motile gametes, from which, however, as the earlier form of reproduction, it may be considered to have been derived. The oogonia and antheridia first appear as small protuberances, which grow out into short lateral branches, and become separated by means of septa from the rest of the thallus (Fig. 297 *o*, *a*). At first, according to OLTMANNS, the rudiment of an

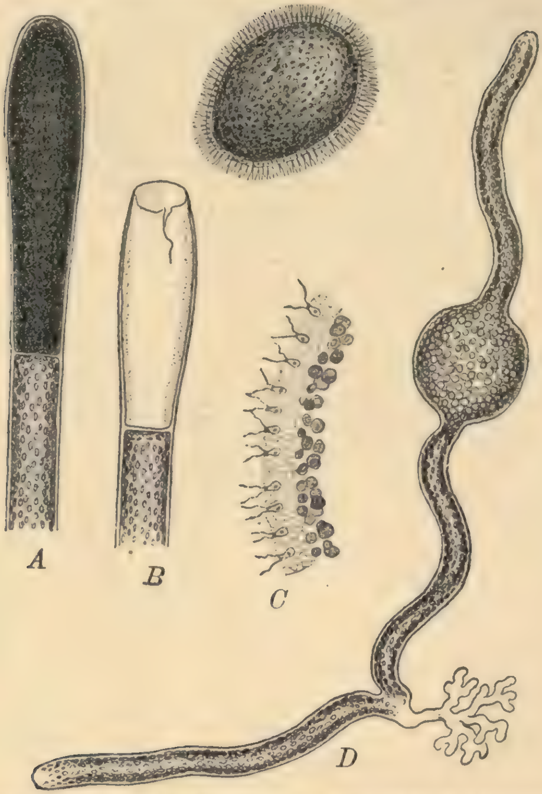


Fig. 296.—*Vaucheria sessilis.* *A*, Young sporangium. *B*, Zoospore with the sporangium from which it has escaped. *C*, A portion of the peripheral zone of a zoospore. *D*, a young plant with rhizoids developed from a zoospore. (*A*, *B*, after Götz; *D*, after Sachs; from Oltmanns' *Algae.* *C*, after Strasburger.)

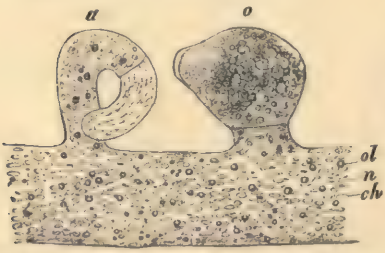


Fig. 297.—*Vaucheria sessilis.* Portion of a filament with an oogonium, *o*; antheridium, *a*; *ch*, chromatophores; *n*, cell nuclei; *ol*, oil globules. (× 240.)

oogonium contains numerous nuclei, of which all but one, the nucleus of the future egg-cell, retreat again into the main filament before the formation of the septum. In *V. geminata* Davis found that all the nuclei, except that of the oosphere, that are in the oogonium degenerated and disappeared. In its mature condition the oogonium has on one side a beak-like projection containing only colourless protoplasm. The oogonium opens at this place, the oosphere rounding itself off. The antheridia, which are also multinuclear, are more or less coiled (*a*), and open at the tip to set free their mucilaginous contents, which break up into a number of swarming spermatozoids. The spermatozoids are very small, and have a single nucleus and two cilia inserted on one side. They collect around the receptive spot of the egg-cell, into which one spermatozoid finally penetrates. After the egg-cell has been fertilised by the fusion of its nucleus with that of the spermatozoid, it becomes invested with a wall and converted into a resting oospore. On germination the oospore grows into a filamentous thallus.

CLASS X

Characeae (Stoneworts) (6, 36)

The Characeae form a sharply defined group of Thallophytes, the origin of which must be looked for in the Chlorophyceae, from which, however, they are distinguished by the complicated structure of their sexual organs. They grow in fresh or brackish water, attached to the bottom and covering extended areas with a mass of vegetation. In some species their cylindrical main axes are over a foot in length, and are composed of long internodes alternating with short nodes, from which short, cylindrical branches are given off in regular whorls with a similar structure, but of limited growth (Fig. 298). The lateral axes are either unbranched or give rise at their nodes to verticillate outgrowths of a second order. From the axil of one of the side branches of each whorl a lateral axis resembling the main axis is produced. The attachment to the substratum is effected by means of branched rhizoids springing from the nodes at the base of the axes.

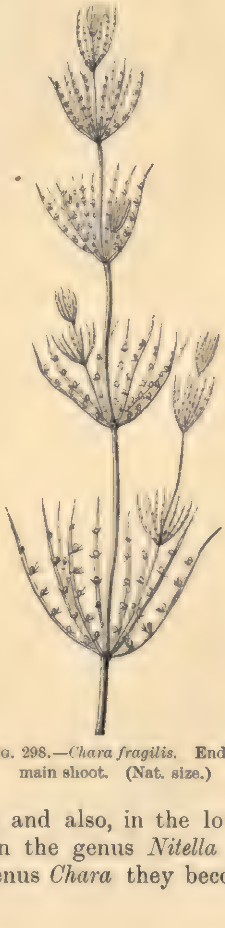


FIG. 298.—*Chara fragilis*. End of main shoot. (Nat. size.)

Both the main and lateral axes grow in length by means of an apical cell, from which other cells are successively cut off by the formation of transverse walls. Each of these cells is again divided by a transverse wall into two cells, from the lower of which a long, internodal cell develops without further division; while the upper, by continued division, gives rise to a disc of nodal cells, the lateral axes, and also, in the lower portion of the main axis, to the rhizoids. In the genus *Nitella* the long internodes remain naked, but in the genus *Chara* they become enveloped by a cortical layer consisting of longitudinal rows of cells which develop at the nodes from the basal cells of the lateral axes.

As a result of the fragmentation of its original nucleus, each internodal cell is provided with a number of nuclei which lie embedded in an inner and actively moving layer of parietal protoplasm. Numerous chloroplasts are found in the internodal cells.

Asexual reproduction by means of swarm-spores or other spores is unrepresented in the Characeae. Sexual reproduction, on the other hand, is provided for by the production of egg-cells and spermatozoids. The female organs are ovate. They are visible to the naked eye, and, like the spherical red-coloured antheridia, are inserted on the nodes of the lateral axes. With the exception of a few diœcious species, the Characeae are monœcious.

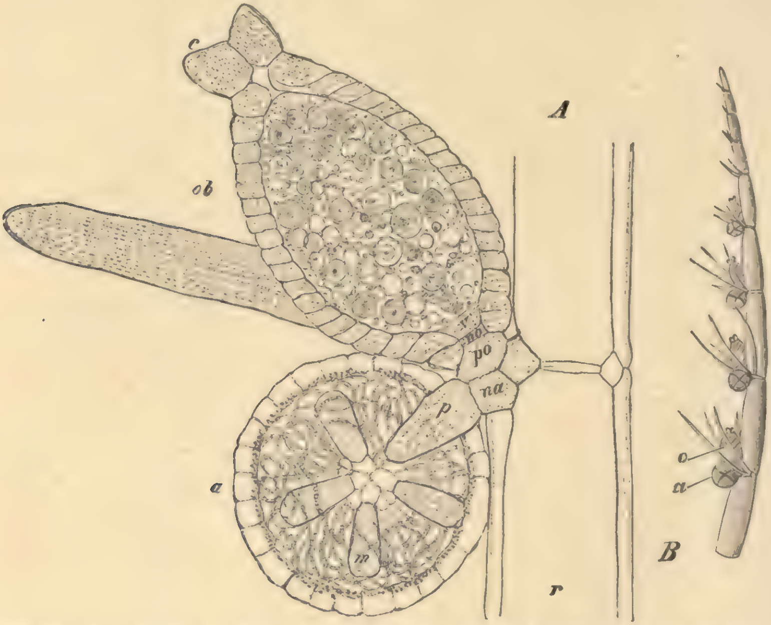


Fig. 299.—*Chara fragilis*. *A*, Median longitudinal section through a lateral axis *r*, and the sexual organs which it bears (× 60); *a*, antheridium borne on the basal nodal cell *na*, by the stalk cell *p*; *m*, manubrium; *ob*, an oogonium; *no*, nodal cell; *po*, the stalk-cell; *v*, pivotal cell; *c*, the crown *B* a lateral axis bearing axes of the third order (× 6); *a*, antheridium; *o*, oogonium.

The oogonia (Fig. 299 *ob*) contain a large ovum, filled with starch grains and oil-drops; this is surrounded by spirally wound tubular cells forming the envelope. These tubes terminate in the crown (*c*) between slits in which the spermatozoids enter. The antheridia (Fig. 299 *a*) possess a wall formed of eight flat cells with infolded walls (shields). From the centre of each of the shields a large cylindrical cell (manubrium) projects into the central cavity, and the inner end of this bears a number of head-cells. The latter bear long septate filaments from each cell of which a spirally wound biciliate spermatozoid is formed. The form of the spermatozoid (Fig. 98 *A*) differs considerably from that of other Algae.

The egg, after fertilisation, now converted into an oospore, becomes invested with a thick, colourless wall. The inner walls of the tubes become thickened and encrusted with a deposit of calcium carbonate, while the external walls of the tubes soon become disintegrated.

In a few cases, *e.g. Chara crinita*, the ovum can develop parthenogenetically without being fertilised. Only female examples of this plant occur in Europe.

The oospore, on germination, gives rise first to a simple, filamentous row of cells, the proembryo. From the first node of the proembryo rhizoids are produced, while at the second node there arise, together with a few simple lateral axes, one or more main axes, which finally develop into a full-grown plant.

The formation of tuber-like bodies (bulbils, starch-stars) on the lower part of the axes is characteristic of some species of the Characeae. These tubers, which are densely filled with starch and serve as hibernating organs of vegetative reproduction, are either modified nodes with much-shortened branch whorls (*e.g.* in *Tolypellopsis stelligera*, when they are star-shaped), or correspond to modified rhizoids (*e.g.* the bulbils of *Chara aspera*).

CLASS XI

Phaeophyceae (Brown Algæ) ($^{6, 20, 37}$)

The Phaeophyceae, like the Chlorophyceae, can be derived from unicellular Flagellata, and in particular from the Chrysomonadinae which possess yellow chromatophores. On to these may be connected unicellular colonial forms like *Phaeococcus*, or forms like *Phaeothamnion* composed of a short filament. The reproduction of these by means of zoospores and conjugating gametes already agrees with that of the simpler Brown Algae.

With the exception of a very few fresh-water species, the Phaeophyceae are only found in salt water. They are all attached, and attain their highest development in the colder waters of the ocean. They show great diversity in the form and structure of their vegetative body. The simplest representatives of this class (*e.g.* the genus *Ectocarpus*) have a filamentous thallus consisting of a branched or unbranched row of simple cells. Some Phaeophyceae, again, have a cylindrical, copiously branched, multicellular thallus (*e.g. Cladostephus*, whose main axes are thickly beset with short multicellular branches (Fig. 7); while in other cases the multicellular thallus is ribbon-shaped and dichotomously branched (*e.g. Dictyota*, Fig. 8). Growth in length in both of these forms ensues from the division of a large apical cell (Figs. 7 and 132). Other species, again, are characterised by disc-shaped or globose thalli.

The Laminariaecae and Fucaceae include the most highly developed forms of the Phaeophyceae. To the first family belongs the genus *Laminaria* found in the seas of northern latitudes. The large-stalked thallus of the Laminarias resembles an immense leaf; it is attached to the substratum by means of branched, root-like holdfasts, developed from the base of the stalk.

In *Laminaria digitata* and *L. Cloustoni* (Fig. 301), a zone at the base of the palmately divided, leaf-like expansion of the thallus retains its meristematic character, and by its intercalary growth produces in autumn and winter a succession of new laminæ. The older lamina becomes pushed up and gradually dies, while a new one takes its place and becomes in turn palmately divided by longitudinal slits. The large size of their thalli is also characteristic of the Laminarias; *L. saccharina* (North Sea), for instance, is frequently 3 m. long and the stalk more than 1 cm. thick.

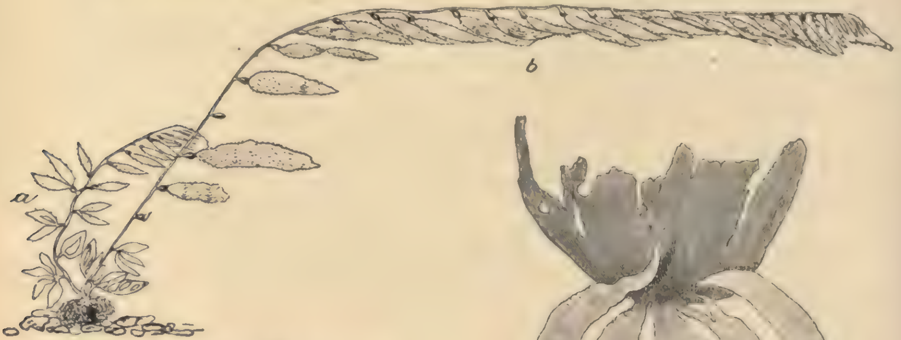


FIG. 300.—*Macrocystis pyrifera*, Ag.; *a*, younger *b*, older thallus. (After SKOTTSBERG. 1/80 nat. size.)

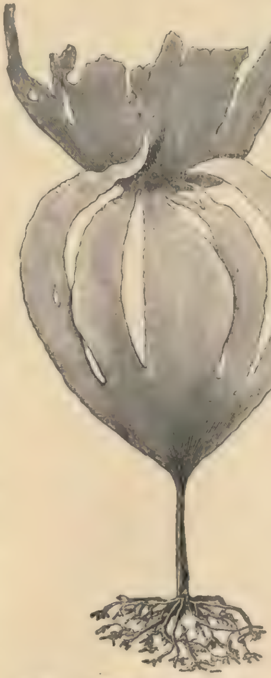


FIG. 301.—*Laminaria Cloustoni*, North Sea. (Reduced to ⅓.)

The greatest dimensions attained by any of the Phaeophyceae are exhibited by certain of the Antarctic Laminariaceae. Of these, *Macrocystis pyrifera* (Fig. 300) is noted for its gigantic size; the thallus grows attached to the sea-bottom at a depth of 2-25 m., and, according to SKOTTSBERG (38), is at first dichotomously branched. Single shoots of the thallus grow to the surface of the water, and floating there attain a length of 70 m.; they bear on one side long flat lobes divided at their free ends, and having at the base of each a large swimming bladder. Other noticeable forms, on account of their tree-like character, are the Antarctic species of *Lessonia*, in which the main axis is as thick as a man's arm; from it are given off lateral branches with hanging leaf-like segments. The plant attains a height of several metres, and has a tree-like habit of growth.

The Fucaceae, although relatively large, do not compare with the Laminariaceae in size. As examples of well-known forms of this order may be cited *Fucus vesiculosus*, which has a ribbon-shaped, dichotomously branching thallus with air-bladders, *Fucus platycarpus* without bladders, and *Fucus serratus* (Fig. 302). They are fastened to the substratum by discoid holdfasts, and growing sometimes over 1 metre long, are found covering extended areas of the littoral region of the sea-coast. *Sargassum*, a related genus chiefly inhabiting tropical oceans, surpasses

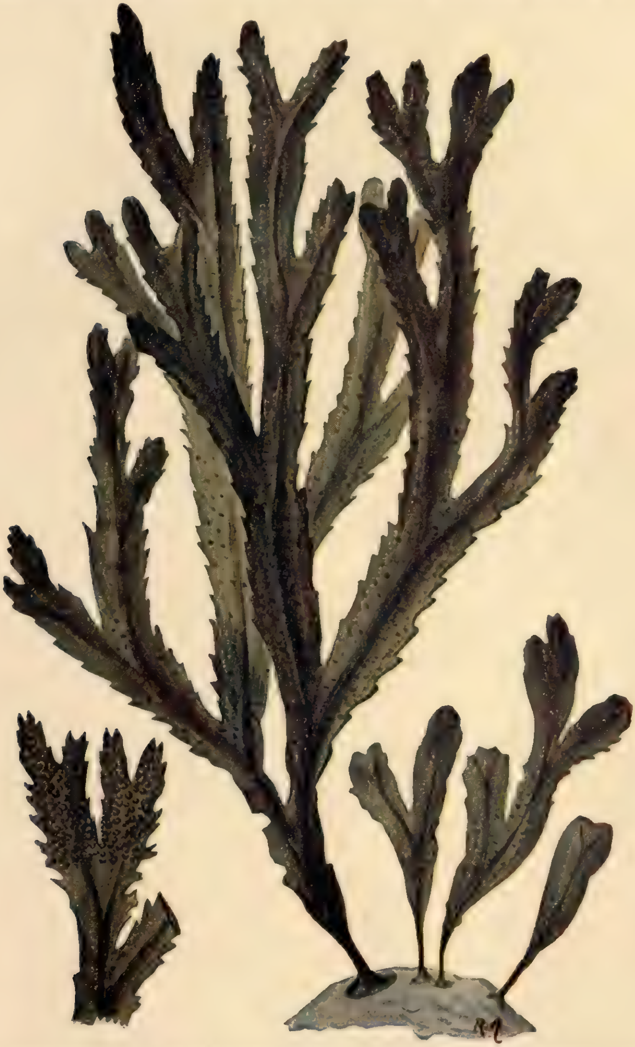


FIG. 302.—*Fucus serratus.* To the left the end of an older branch bearing conceptacles. (⅓ nat. size.)

the other Brown Seaweeds, and even all other Algae, in the segmentation of its thallus. The thallus of *Sargassum* shows, in fact, a distinction into slender, branched, cylindrical axes with lateral outgrowths, which, according to their function, are differentiated as foliage, bracteal, or fertile segments, or as air-bladders. Various species of *Sargassum* which have been swept away from the coast by currents finally collect in large floating masses in quiet regions of the ocean (Sargasso Sea).

The cells of the Phaeophyceae have usually but one nucleus. They contain a larger or smaller number of simple or lobed, disc-shaped chromatophores, which contain a brown pigment (phaeophyll, p. 62), giving to the algae a yellowish-brown or dark brown colour. Numerous grains of a semi-fluid substance, to which the name fucosan has been given, appear as the product of assimilation. This substance appears to be a carbohydrate, and, according to HANSTEEN (39), originates in the chromatophores. Among the more highly developed forms the thallus exhibits a highly differentiated anatomical structure. The outer cell layers, as a rule, function as an assimilatory tissue, the inner cells as storage reservoirs. In some species the axial cells of the thallus are arranged in strands containing sieve-tubes (40).

Two orders of Phaeophyceae may be distinguished. The Phaeosporeae are vegetatively reproduced by means of zoospores and sexually by ciliated gametes; they thus resemble *Ulothrix* among the Green Algae. The Cyclosporeae show a marked differentiation of their sexual cells into large, naked, non-motile, spherical oospheres and small, ciliated spermatozoids; some forms are also asexually reproduced by means of naked, non-motile spores.

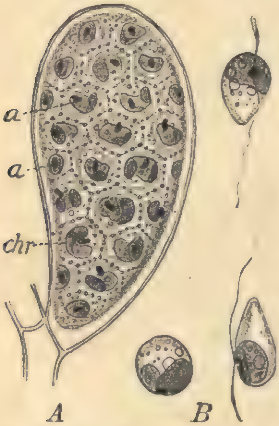


FIG. 303.—*A*, *Pleurocladia lacustris*. Unilocular sporangium with its contents divided up into the zoospores; *a*, eye-spot; *chr*, chromatophore. (After KLEBAHN.) *B*, *Chorda filum*. Zoospores. (After REINKE.) (From OLTMANNS' *Algae*.)

Order 1. Phaeosporeae (41)

In this order are included the Laminarias, as well as the majority of the other Phaeophyceae. Asexual multiplication is effected by means of swarm-spores, which are produced in large numbers in simple, so-called unilocular sporangia; they have a red eye-spot, a chromatophore, and two LATERALLY INSERTED cilia (Fig. 303); one directed forwards and the other backwards. Only this asexual reproduction is yet known in the Laminariaceae.

In addition to unilocular sporangia, multilocular sporangia are produced in the Phaeosporeae (Fig. 304). Each cell of the latter produces a single swarm-spore, rarely several. The conjugation of these swarm-spores has been observed in some genera. On this account these swarm-spores must be termed gametes, and the corresponding sporangia gametangia. The degree of sexual differentiation varies, and in some cases the swarm-spores produced in multilocular sporangia can germinate without conjugating, as was seen to occur in *Ulothrix* among the Chlorophyceae.

Ectocarpus siliculosus (Fig. 305) will serve as an example of the mode of conjugation of gametes produced from multilocular gametangia. The gametes are similar in form, but their different behaviour allows of their distinction into male and female which are formed in distinct gametangia, borne on the same or different plants. The female gamete becomes attached to a substratum, and numerous male gametes gather around it (Fig. 305, 1). Ultimately a male gamete fuses with the female to form a zygote (Fig. 305, 2-9). This contains after the fusion a single nucleus, but two chromatophores, and soon becomes attached and surrounded by a cell-wall; it grows into a new plant.

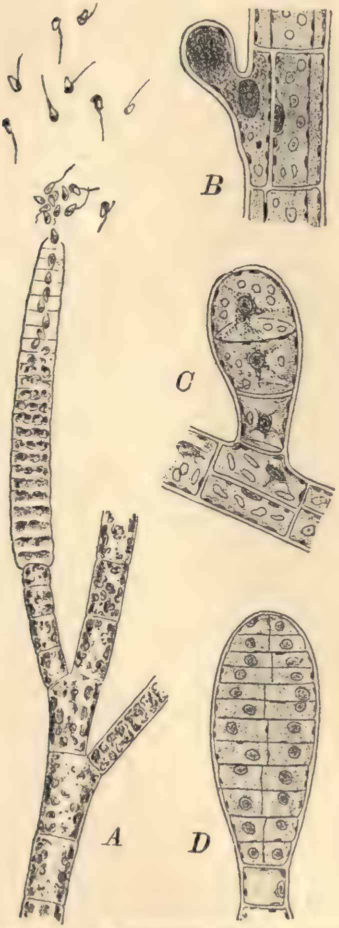


FIG. 304.—*A*, *Ectocarpus siliculosus*. Plurilocular sporangium liberating its contents (after THURET). *B*, *C*, *D*, *Sphacelaria cirrhosa*, development of the plurilocular sporangium (after REINKE). (From OLTMANNS' *Algae*.)

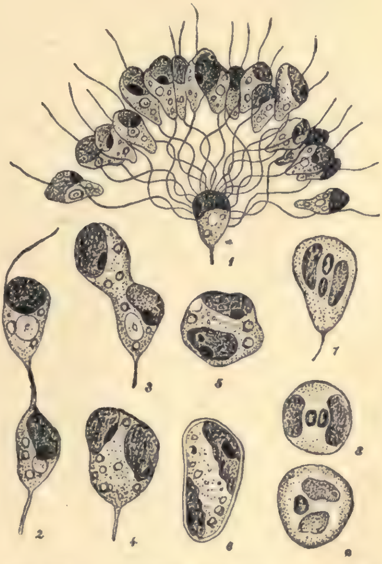


FIG. 305.—*Ectocarpus siliculosus*. *1*, Female gamete surrounded by a number of male gametes; seen from the side. *2-5*, Stages in the fusion of gametes. *6*, Zygote after 24 hours. *7-9*, Fusion of the nuclei in conjugation, as seen in fixed and stained material. (*1-5*, after BERTHOLD; *6-9*, after OLTMANNS.)

In other Phaeophyceae the distinction between the two kinds of gametes is expressed in their shape and size. The Cutleriaceae afford a particularly good transition from isogamy to oogamy (42).

Order 2. Cyclosporeae

Family 1. Dictyotaceae (43, 44).—Only a small number of forms belong to this family. *Padina pavonia*, which occurs in the Mediterranean, and *Dictyota dichotoma*, which is widely spread in the European seas (Fig. 8), are examples. They are distinguished from the Fucaceae by bearing asexual and sexual organs on distinct individuals. The spores are formed as in the Red Algae in sporangia; usually there are four spores (tetraspores), less commonly eight. They have no cell-walls and are unprovided with cilia and must be termed aplanospores (Fig. 306, 1). The oogonia and antheridia in *Dictyota* are grouped in sori (Fig. 306, 2, 3) and arise from adjacent cortical cells each of which divides into a stalk cell and the oogonium (or antheridium). The peripheral cells of the antheridial group remain sterile and form a kind of indusium. Each oogonium forms a single uninucleate oosphere, the antheridia become septate, resembling the plurilocular gametangia, and each cell gives rise to a spermatozoid. This, in contrast to the spermatozoids of other Brown Algae, has a single long cilium inserted laterally.

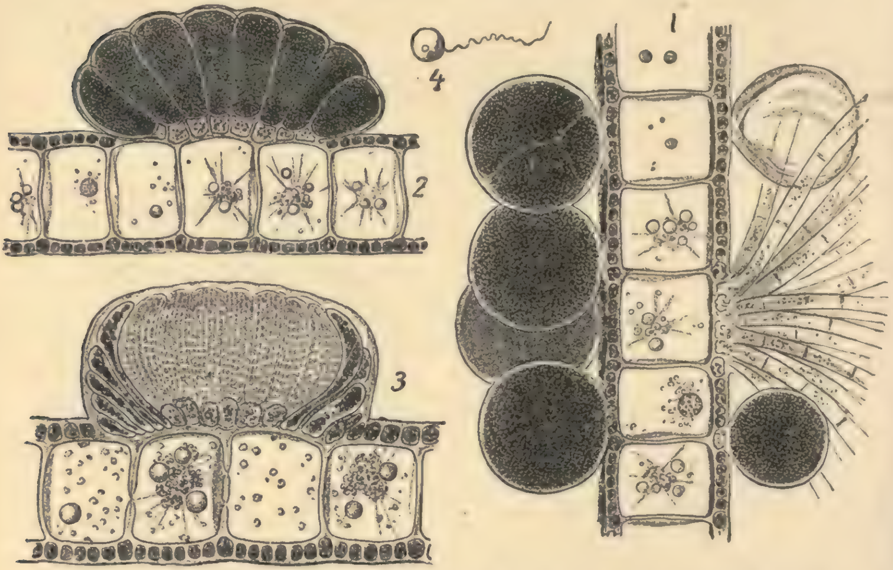


FIG. 306.—*Dictyota dichotoma*. Transverse sections of the thallus. *1*, With tetrasporangia; *2*, with a group of oogonia; *3*, with a group of antheridia (after THURET). *4*, Spermatozoid (after WILLIAMS). (From OLTMANNS' *Algae*.)

Dictyota is diœcious. The male and female plants arise from the asexually produced tetraspores; from the fertilised ovum plants which bear tetraspores are developed. In the tetrad division in the sporangia the number of chromosomes becomes reduced from 32 to 16, and the reduced number is maintained in all the nuclei of the sexual plants, the double number being again attained in fertilisation. There is thus (in contrast to the condition of things in the Phaeosporeae) a true alternation of generations. The sexual generation (gametophyte) and the asexual generation (sporophyte) do not, however, show differences in structure as is the case in the Bryophyta and Pteridophyta.

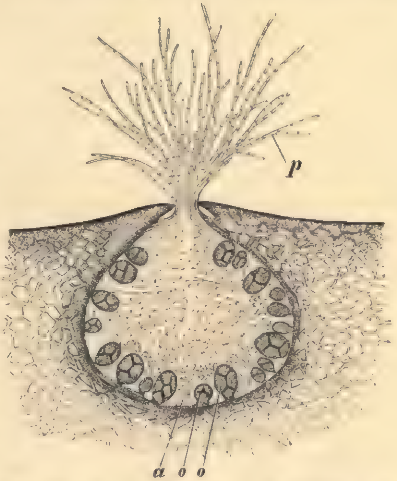


FIG. 307.—*Fucus platycarpus*. Monœcious conceptacle with oogonia of different ages (*o*), and clusters of antheridia (*a*); *p*, paraphyses. (After THURET, × circa 25.)

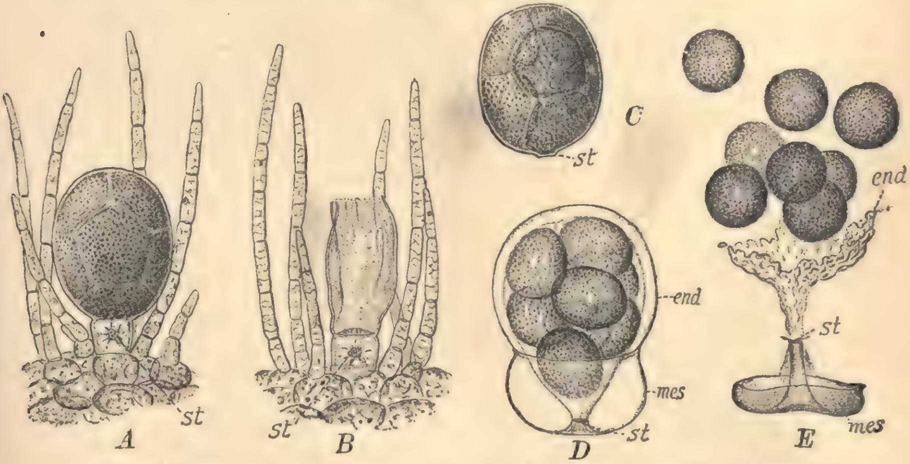


FIG. 308.—*A*, Oogonium, the contents of which have divided into the eight egg-cells. *B*, Oogonium, from which the contents (*C*) have been extruded. *D*, *E*, Liberation of the eight egg-cells. *st*, stalk-cell ; *mes*, middle, and *end*, inner layers of the oogonial cell-wall. (After THURET. From OLTMANNS' *Algae*.)

Family 2. Fucaceae (^{45}).—Asexual reproduction is wanting in this order, while sexual reproduction is distinctly oogamous. The oogonia and antheridia of *Fucus* are formed in special flask-shaped depressions termed CONCEPTACLES, which are crowded together below the surface in the swollen tips of the dichotomously branched thallus (cf. *F. serratus*, Fig. 302). The conceptacles of *F. platycarpus* (Fig. 307) contain both oogonia and antheridia, while *F. vesiculosus*, on the contrary, is diœcious. From the inner wall of the conceptacles, between the oogonia and antheridia, spring numerous unbranched, sterile hairs or PARAPHYSES, of which some protrude in tufts from the mouth of the conceptacle (Fig. 307 *p*). The antheridia are oval in shape, and are formed in clusters on special short and much-branched filaments (Figs. 307 *a*, 309, 1, 2). The contents of each antheridium separate into a large number of spermatozoids, which are discharged in a mass, still enclosed within the inner layer of the antheridial wall (Fig. 309, 4). Eventually set free from this outer covering, the spermatozoids appear as somewhat elongated, ovate bodies, having two lateral cilia of unequal length and a red eye-spot. The oogonia (Figs. 307 *o*, 308) are nearly spherical, and are borne on a short stalk consisting of a single cell. They are of a yellowish-brown colour, and enclose eight spherical egg-cells which are formed by the division of the oogonium mother cell. The eggs are enclosed within a thin membrane when ejected from the oogonium (Fig. 308 *B*, *C*). This membranous envelope deliquesces at one end and, turning partly inside out, sets free the eggs (*D*, *E*). The spermatozoids then gather round the eggs in such numbers that by the energy of their movements they often set them in rotation (Fig. 309, 5). After an egg has been fertilised by the entrance of one of the spermatozoids (Fig. 309, 6) it becomes invested with a cell-wall, attaches itself to the substratum, and gives rise by division to a new plant.

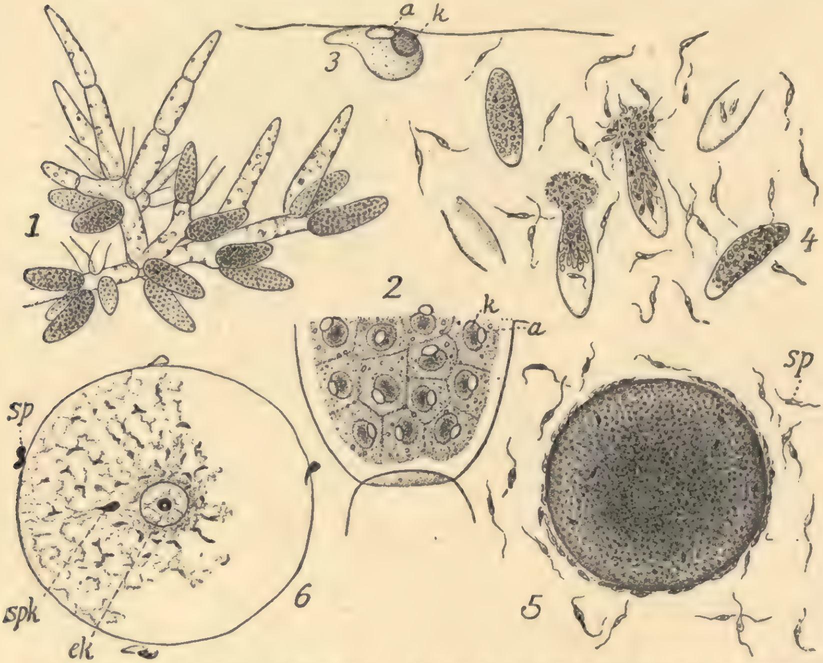


FIG. 309.—*Fucus*. *1*, Group of antheridia. *2*, Part of an antheridium showing developing spermatozoids. *3*, Spermatozoid : *a*, eye-spot ; *k*, nucleus. *4*, Isolated antheridia liberating the spermatozoids. *5*, Oosphere surrounded by spermatozoids. *6*, Section through a fertilised egg : *ek*, nucleus of egg ; *spk*, sperm-nucleus ; *sp*, spermatozoids. (*1*, *4*, *5*, after THURET ; *2*, *3*, after GUIGNARD ; *6*, after FARMER. From OLTMANNS' *Algae*.)

In the case of other Fucaceae which produce four, two, or even only one egg in their oogonia, the nucleus of each oogonium, according to OLTMANNS, nevertheless first divides into eight daughter nuclei, of which, however, only the proper number give rise to eggs capable of undergoing fertilisation.

Since the Fucaceae have no asexual spore-formation the alternation of generations characteristic of *Dictyota* is wanting in them. It is possible to regard the divisions leading to the development of the sexual cells in the oogonium and antheridium, in which the reduction of chromosomes takes place, as corresponding to a reduced sexual generation. On this view the thallus of *Fucus* would correspond to the sporophyte of *Dictyota*, and the young sexual organs would be equivalent to the tetrasporangia of the latter ([44]).

Economic Uses.—The dried stalks of *Laminaria digitata* and *L. Cloustoni* are used as dilating agents in surgery. IODINE is obtained from the ash (varec, kelp) of various Laminariaceae and Fucaceae, and formerly soda was similarly obtained. Many Laminarias are rich in MANNITE (*e.g. Laminaria saccharina*), and are used in its production, and also as an article of food by the Chinese and Japanese.

CLASS XII

Rhodophyceae (Red Algae) ([6, 20, 46])

The Rhodophyceae or Florideae constitute an independent group of the higher Algae, the phylogenetic origin of which is perhaps to be sought among the higher Green Algae. They are almost exclusively marine, and specially characterise the lowest algal region on the coasts of all oceans, especially in temperate and tropical

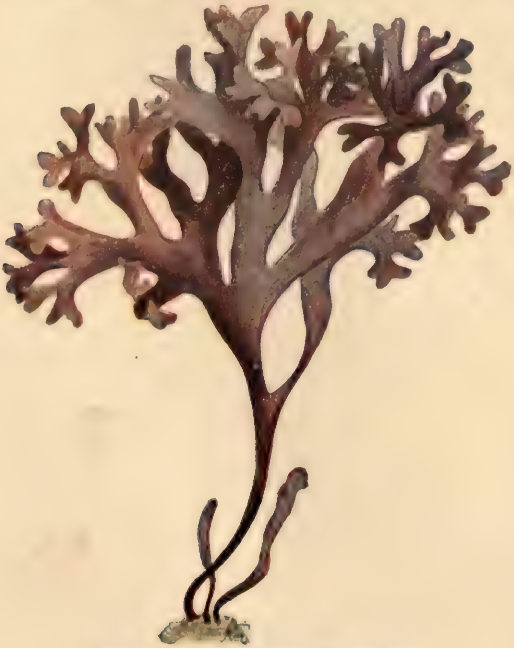


FIG. 310.—*Chondrus crispus.* (½ nat. size.)

latitudes. A few genera (*e.g. Batrachospermum*, *Lemanea*) grow in fresh-water streams.

The thallus of the Red Algae exhibits a great variety of forms. The simplest forms are represented by branched filaments consisting of single rows of cells (*e.g. Callithamnion*). In other cases the branched filamentous thallus appears multicellular in cross-section. In many other forms the thallus is flattened and ribbon-like (*e.g. Chondrus crispus*, Fig. 310; *Gigartina mammillosa*, Fig. 311); while in other species it consists of expanded cell surfaces attached to a substratum.

One of the more complicated forms is *Delesseria sanguinea* (*Hydrolapathum*) (Fig. 9), which occurs on the coasts of the Atlantic. The leaf-like thallus which springs from an attaching disc is provided with mid ribs and lateral ribs. In the autumn the wing-like expansions of the thallus are lost, but the main ribs persist and give rise to new branches in the succeeding spring. All the Florideae are attached at the base by means of rhizoidal filaments or discoid holdfasts. The thalli of the Corallinaceae, which have the form of branched filaments or of flattened or tuberculate incrustations, are especially characterised by their coral-like appearance, owing to the large amount of calcium carbonate deposited in their cell-walls. The calcareous Florideae are chiefly found on coasts exposed to a strong surf, especially in the tropics.

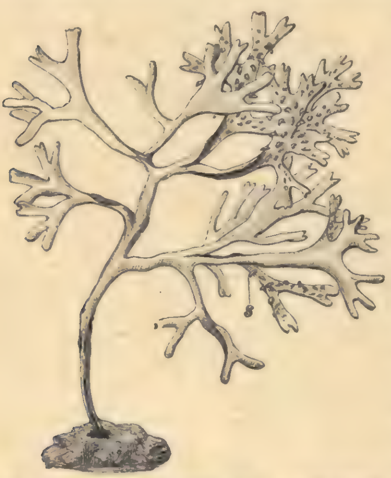


Fig. 311.—*Gigartina mammillosa*. *s*, Wart-shaped cystocarps. (¾ nat. size.)

The Rhodophyceae are usually red or violet; sometimes, however, they have a dark purple or reddish-brown colour. Their chromatophores, which are flat, discoid, oval, or irregular-shaped bodies and closely crowded together in large numbers in the cells, contain a red pigment, PHYCOERYTHRIN, which completely masks the chlorophyll and appears to be chemically combined with it (p. 62). True starch is never formed as a product of assimilation, its place being taken by other substances, very frequently, for example, by Floridean starch, in the form of spherical stratified grains which stain red with iodine. Oil-drops also occur. The cells may contain one or several nuclei.

Reproduction is effected either asexually by means of spores, or sexually by the fertilisation of female organs by male cells.

The asexual SPORES are non-motile; they have no cilia and are simply naked, spherical cells. They are produced, usually, in groups of four, by the division of a mother cell or sporangium, from which they are in time set free by the transverse rupture of its walls. The sporangia themselves are nearly spherical or oval bodies seated on the thalloid filaments or embedded in the thallus. The spores escape by a transverse rupture of the wall of the sporangium. In consequence of their usual formation in fours, the spores of the Florideae are termed TETRASPORES (Fig. 312). They are analogous to the swarm-spores of other Algae; similar spores are found also in the Dictyotaceae among the brown Algae.

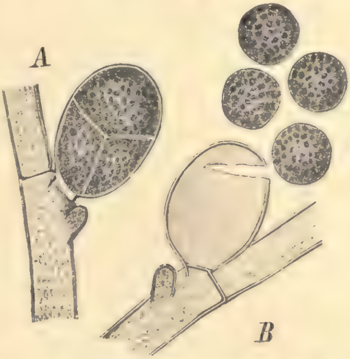


FIG. 312.—*Callithamnion corymbosum.* *A*, Closed sporangium; *B*, empty sporangium with four extruded tetraspores. (After THURET.)

In the construction of the sexual organs, particularly the female, the Rhodophyceae differ widely from the other Algae. *Batrachospermum moniliforme*, a freshwater form, may serve as an example to illustrate the mode of their formation. This Alga possesses a brownish thallus, enveloped in mucilage, and consisting of verticillately branched filaments. The sexual organs appear in the autumn and form on the branching whorls glomeruli or spherical bodies composed of short, radiating branches.

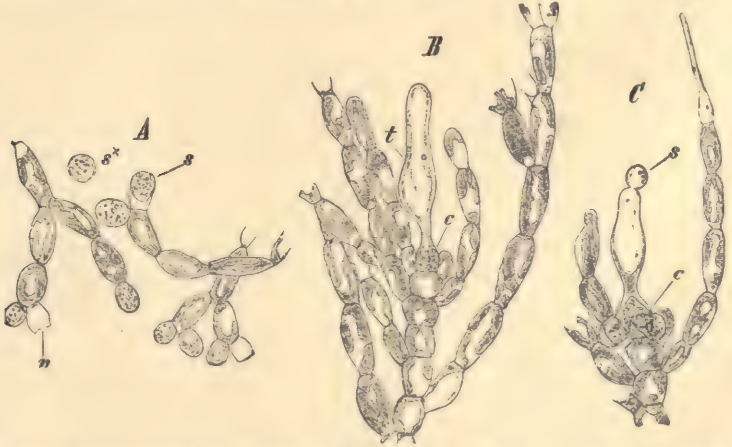


FIG. 313.—*Batrachospermum moniliforme.* *A*, Male branch with antheridia, isolated by pressure; *s**, a spermatium; *s*, a spermatium escaping from an antheridum; *v*, an empty antheridium. *B*, female branch with an unfertilised carpogonium; *c*, basal portion; *t*, trichogyne of carpogonium. *C*, female branch with fertilised carpogonium; *s*, the spermatium after the fusion of its contents with the trichogyne; *c*, fertile filaments developing from the basal portion of the carpogonium. (× 540.)

The antheridia, also known as spermatangia (Fig. 313 *A*), are produced, usually in pairs, at the ends of the radiating branches of a glomerulus. Each antheridium consists of a single thin-walled cell, in which the whole of the protoplasm, as is the rule in all Rhodophyceae, is consumed in the formation of one uninuclear SPERMATIUM; according to some authors the nucleus of the spermatium divides into two. The spermatia are nearly spherical, and are invested with a thin outer membrane or cell wall. They are non-motile, unlike the ciliated spermatozoids of the other Algae, and have therefore received a distinctive name. In consequence of their incapacity for independent movement, they must be carried passively by the water to the female organs, which are situated near the antheridia at the ends of other branches. The female organ is called a CARPOGONIUM (Fig. 313 *B*), and consists of an elongated cell with a basal, flask-shaped portion (*c*) prolonged into a filament, termed the TRICHOGYNE (*t*). The basal portion contains the nucleus of the egg and the chromatophores, while the trichogyne functions as a receptive organ for the spermatia, one or two of which fuse with it, and the contents, escaping through the spermatium wall, pass into the carpogonium. The sperm nucleus passes down the trichogyne and fuses with the nucleus of the egg-cell. The fertilised egg, which becomes limited from the trichogyne by a wall, does not become converted directly into an oospore, but, as a result of fertilisation, numerous branching sporogenous filaments grow out from the sides of the ventral portion of the carpogonium. At the same time, by the development of outgrowths from cells at the base of the carpogonium an envelope is formed about the sporogenous filaments. The whole product of fertilisation, including the surrounding envelope, constitutes the fructification, and is termed a CYSTOCARP. The profusely-branched sporogenous filaments become swollen at the tips and give rise to spherical, uninuclear spores known as CARPOSPORES, which are eventually set free from the envelope. In the case of *Batrachospermum* the carpospores produce a filamentous protonema, the terminal cells of which give rise to asexual unicellular spores. These spores serve only for the multiplication of the protonema. Ultimately, however, one of the lateral branches of the protonema develops into the sexually differentiated filamentous thallus. The production of spores by the protonema is analogous to the formation of tetraspores by other Florideae.

The formation of the cystocarps and carpospores is much more complicated in the case of other genera, but in all cases, according to OLTMANNS, the carpospores are descended from the fertilised egg-cell. There are thus two generations distinguishable in the life-history of the Florideae, the sexual (gametophyte), which bears the egg-cells and the spermatia, and the asexual generation (sporophyte), derived from the fertilised egg-cell; the latter generation, which produces the carpospores, remains in connection with the parent plant. This type of alternation of generations is comparable with that found in Mosses and Ferns. The production of tetraspores is an asexual mode of reproduction of the sexual generation and precedes the formation of the sexual organs.

Dudresnaya coccinea, which is found on the warmer coasts of Europe, has a branched, cylindrical thallus and will serve as an example of the more complicated mode of origin of the spore-bearing generation (Fig. 314). The carpogonial branches consist of about seven cells, the terminal one bearing a very long trichogyne. After fertilisation the carpogonial cell grows out into a filament, which elongates and becomes branched. This filament fuses with a number of special cells, characterised by their abundant contents, the AUXILIARY CELLS. The first of these lie in the carpogonial branch itself, the others in adjoining lateral branches. All the nuclei of the sporogenous filament are derived by division from that of the fertilised egg-cell. The successive fusions with auxiliary cells do not involve nuclear fusions, but simply serve to nourish the sporogenous filament. A second and third sporogenous filament may arise from the carpogonial cell.

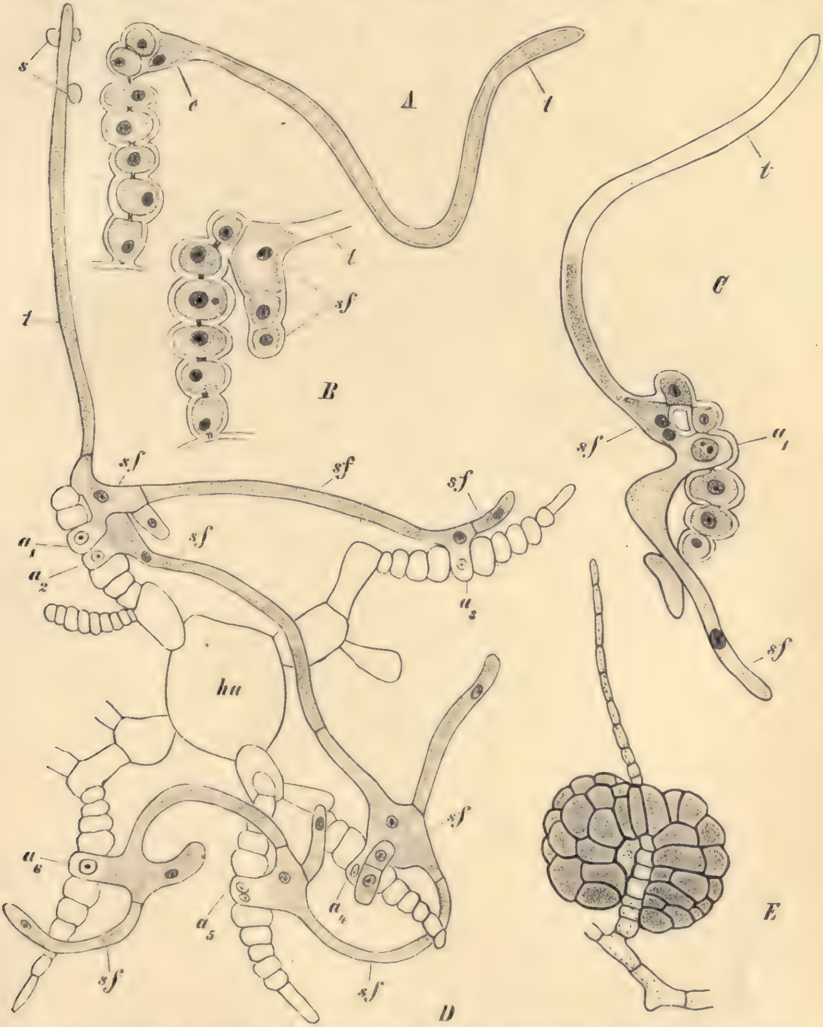


FIG. 314.—*Dudresnaya coccinea.* *A* Carpogonial branch ; *c*, carpogonium ; *t*, trichogyne. *B*, carpogonium after fertilisation, grown out into the sporogenous filament (*sf*). *C*, fusion of the sporogenous filament with the first auxiliary cell (a_1). *D*, branching of the filament and fusion with six auxiliary cells (a_1-a_6) ; the cells a_3-a_6 are borne on branches originating from the axis *ha* (diagrammatic). *E*, Ripe cluster of carpospores originating from one branch. (*A*-*D*, after OLTMANNS ; *E*, after BORNET. *A*-*C*, × about 500 ; *D*, × 250 : *E*, × 300.)

Two outgrowths now arise from each of the swollen cells of the sporogenous filament which fused with auxiliary cells. By further division of these outgrowths the spherical masses of carpospores, which subsequently become free, are derived (Fig. 314 *E*).

Harveyella mirabilis (^{47}), one of the Florideae occurring in the North Sea, is of special interest. It grows as a parasite on another red seaweed, *Rhodomela subfusca*, on which it appears in the form of a small white cushion-like growth. As a result of its parasitic mode of life the formation of chromatophores has been entirely suppressed, and thus this plant behaves like a true Fungus.

Economic Uses.—*Gigartina mammillosa* (Fig. 311), with peg-like cystocarps 2-5 mm. in length, and *Chondrus crispus* (Fig. 310), with oval cystocarps about 2 mm. long, sunk in the thallus, tetraspores in groups on the terminal segments of the thallus. Both forms occur in the North Sea as purplish-red or purplish-brown Algae ; when dried they have a light yellow colour, and furnish the official CARRAGHEEN, "Irish Moss," used in the preparation of jelly. AGAR-AGAR, which is used for a similar purpose, is obtained from various Florideae ; *Gracilaria lichenoides* supplies the Agar of Ceylon (also called *Fucus amylaceus*), *Eucheuma spinosum*, the Agar of Java and Madagascar.

CLASS XIII

Phycomycetes ($^{48, 49, 50}$)

In the nature both of their thallus and sexual organs the Phycomycetes exhibit a close connection with the Siphoneae. The phylogenetic origin of most of the Phycomycetes must be sought in this group, though certain forms point to a relationship with other Green Algae (*e.g. Basidiobolus* with the Conjugatae). They can only for the present be regarded as a definite class, pending their separation into several series derived from distinct classes of Algae.

The thallus consists of extensively branched tubular threads in which, as is the case in *Vaucheria*, transverse septa only form in connection with the reproductive organs. The continuous protoplasmic mass contains numbers of very small nuclei, but chromatophores are entirely wanting in these colourless organisms. The whole thallus of a Fungus is spoken of as the mycelium, the individual filaments as hyphæ. In the Phycomycetes the hyphæ are non-septate, their division into distinct cells only taking place in a few cases. The plants are either saprophytes occurring on the putrefying remains of animals or plants in water or on decaying organic substances exposed to air, or they live parasitically in the tissues of higher plants or on insects.

Asexual reproduction is effected by means of spores. These are formed in the majority of the genera within sporangia, the protoplasm of which splits into the numerous spores. The latter escape in the genera which live in water as ciliated swarm-spores (Fig. 316) ; in the forms which are exposed to the air the spores are enclosed in a cell wall (Fig. 323). The conidia, which are sometimes found together with sporangia, in other cases alone, are also adapted for dispersal in air. They arise by a process of budding and abstriction from the ends of certain hyphæ which are usually raised above the substratum as special conidiophores.

The sexual organs of the Phycomycetes are in many ways peculiar, and the two groups of the Oomycetes and the Zygomycetes are distinguished according to their nature. In the Oomycetes, which stand nearer to the Green Algae, oogonia and antheridia are found; the contents of the latter enter the oogonium by means of a tubular outgrowth, and after fertilisation oospores are formed. In *Monoblepharis* alone are free spermatozoids found. The sexual organs of the Zygomycetes are alike, and on conjugation a zygospore is produced. They are usually multinucleate and thus are morphologically comparable to a whole gametangium of an isogamous Alga.

Multinucleate gametangia, oogonia, and antheridia, which fuse directly with one another, without the separation and escape of the individual gametes, are generally termed CŒNOGAMETES.

Order 1. Oomycetes

1. Only in the small family of the **Monoblepharideae** (51) are free ciliated spermatozoids liberated from the antheridia. In the other Oomycetes the multinucleate contents of the antheridium do not divide into separate spermatozoids, but are directly introduced into the egg-cell by means of an outgrowth of the antheridium.

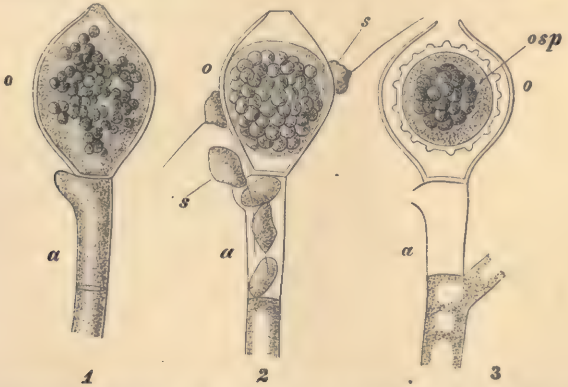


FIG. 315.—*Monoblepharis sphaerica.* End of filament with terminal oogonium (*o*) and an antheridium (*a*): 1, before the formation of the egg-cells and spermatozoids; 2, spermatozoids (*s*) escaping and approaching the opening of the oogonium; 3, *osp*, ripe oospore, and an empty antheridium. (After CORNU, × 800.)

The species of *Monoblepharis* live in water upon decaying remains of plants. Asexual reproduction is effected by means of swarm-spores, formed in large numbers in sporangia. The oogonium, which is usually terminal, contains only a single egg-cell (Fig. 315). The antheridia, which resemble the sporangia, liberate a number of uniciliate spermatozoids. On a spermatozoid reaching the egg-cell through an opening in the tip of the oogonium an oospore is formed. A spinous cell wall forms around the oospore.

2. The **Saprolegniaceae** (52), which connect on to the preceding family, live like them saprophytically on the surface of decaying plants and insects and even on living fishes. Asexual propagation is effected by club-shaped sporangia (Fig. 316) which produce numerous biciliate swarm-spores. The sexual organs develop on older branches of the mycelium (Fig. 317 *a*). The oogonia give rise to a larger (as many as 50) or smaller number of egg-cells, rarely only to a single one. At first the egg-cell contains numerous nuclei, but usually all but the single nucleus of the egg degenerate. The tubular, multinucleate antheridia apply themselves to the oogonia and send fertilising tubes to the egg-cells. One male nucleus enters the egg-cell and fuses with its nucleus (Fig. 318). The oospore after fertilisation acquires a thick wall. In some forms belonging to this family and to the Peronosporeae the formation of antheridia is occasionally or constantly suppressed; the oospores develop parthenogenetically without being fertilised (Fig. 317).

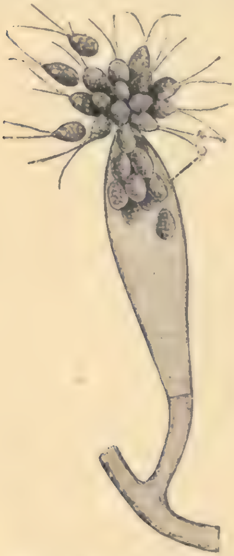


FIG. 316. — *Saprolegnia mixta.* The biciliate zoospores, s^2, are escaping from the sporangium.

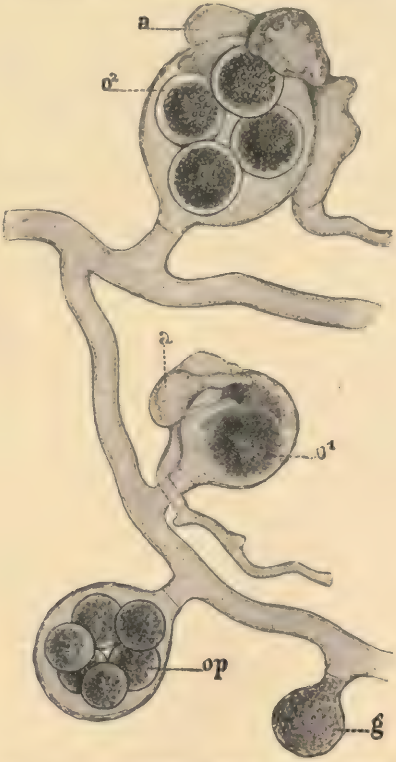


FIG. 317. — *Saprolegnia mixta.* Hyphæ bearing the sexual organs; *a*, antheridium which has sent a fertilisation tube into the oogonium; o^1, egg-cell; o^2, oospore enclosed in a cell-wall; *op*, parthogenetic oospores; *g*, young oogonium. (After G. KLEBS.)

3. The **Chytridiaceae** (53) are microscopically small Fungi parasitic on aquatic or

land plants and in some cases on animals. The non-septate mycelium is feebly developed, and is frequently reduced to a single sac-shaped cell inhabiting a cell of the host. Asexual multiplication is effected by means of swarm-spores provided with one or two cilia. In the simplest forms the entire cell becomes converted into the sporangium. *Olpidium Brassicae* (Fig. 319), which is parasitic in the tissues of the base of the stem of young cabbage plants and brings about their death, may be taken as an example. The sporangia in this case have a long neck from which the swarm-spores escape. Thick-walled sporangia which undergo a resting period are also frequently found in the Chytridiaceae.

Sexual reproduction is only found in some of the genera, in the form of fusion of an antheridium with an oogonium and the production of an oospore. The systematic position of the Chytridiaceae among the Phycomycetes is still doubtful; the simplest forms appear to have originated in part from Flagellatae and partly from Protococcaceae.

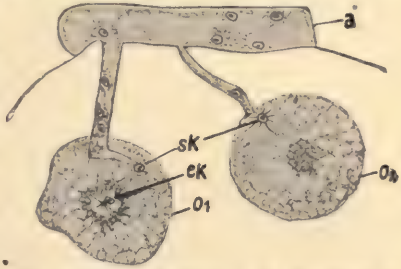


FIG. 318.—*Achlya polyandra.* The fertilisation of two egg-cells, *o*, of an oogonium by two tubes from the antheridium *a*; *ek*, nucleus of the egg-cell; *sk*, sperm-nucleus; in o^2 the section has not passed through the egg-nucleus. (After TROW.)

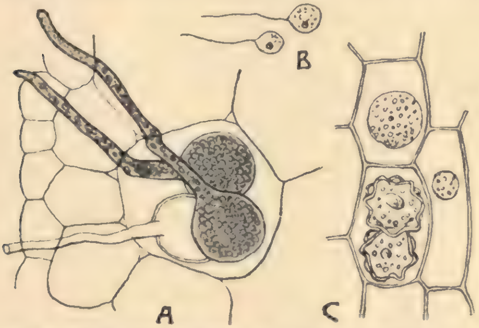


FIG. 319.—*Olpidium Brassicae.* *A*, Three zoosporangia, the contents of one of which has escaped (× 160). *B*, Zoospores (× 520). *C*, Resting sporangia (× 520). (After WORONIN.)

4. The **Peronosporeae** (54) are parasitic Fungi whose mycelium penetrates the tissues of the higher plants, and is frequently the cause of death. In damp climates, certain species occasion epidemic diseases in cultivated plants. Thus, the mycelium of *Phytophthora infestans*, the fungus which causes the Potato disease, lives in the intercellular spaces of the leaves and tubers of the Potato plant, and by penetrating the cells with its short haustoria it leads to the discoloration and death of the foliage and tubers. Sexual reproductive organs have not as yet been observed in this species. Asexual, oval sporangia are formed on long branching sporangiophores which grow out of the stomata, particularly from those on the under side of the leaves (Fig. 320), and appear to the naked eye as a white mould. The sporangia, at first terminal, are cut off by transverse walls from the ends of the branches of the sporangiophore, by the subsequent growth of which they become pushed to one side, and so appear to be inserted laterally. Before any division of their contents has taken place, the sporangia (*B*) fall off and are disseminated by the wind; in this way the epidemic becomes widespread. The development of swarm-spores in sporangia is effected only in water, and is consequently possible only in wet weather. In this process the contents of the sporangium divide into several biciliate swarm-spores (*C*, *D*). Each

of these spores after escaping from the sporangium gives rise to a mycelium, which penetrates the tissues of a leaf. The sporangium may also germinate directly without undergoing division and forming swarm-spores. A similar transformation of sporangia into conidia is also found in other Peronosporeae as a result of their transition from an aquatic to a terrestrial mode of life.

Plasmopara viticola, an extremely destructive parasite, also produces copiously branched sporangiophores and occasions the "False Mildew" of the leaves and fruit of the Grape-vine. *Albugo candida* (= *Cystopus candidus*), another very common species, occurs on Cruciferae, in particular on *Capsella bursa pastoris*, causing white swellings on the stems. In this species the sporangia are formed in long chains on the branches of the mycelium under the epidermis of the host plant, and produce numerous swarm-spores.

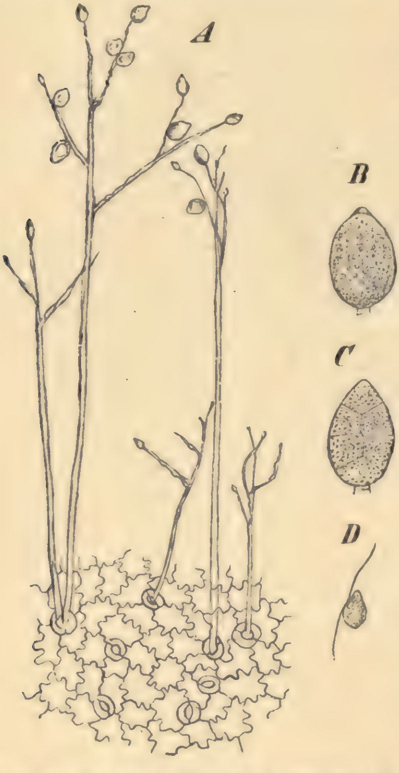


FIG. 320.—*A*. Surface view of the epidermis of a potato leaf, with sporangiophores of *Phytophthora infestans* projecting from the stomata (× 90); *B*, a ripe sporangium; *C*, another in process of division; *D*, a swarm-spore. (*B-D* × 540.)

The sexual organs of the Peronosporeae resemble those of the genus *Vaucheria* (Fig. 292). They arise within the host plant—the oogonia as spherical swellings of the ends of certain hyphæ, the antheridia as tube-like outgrowths arising as a rule just below the oogonia. Both are cut off by transverse walls and are multinucleate (Fig. 321). The several species exhibit interesting differences as regards the nuclear changes. In *Peronospora parasitica*, *Albugo candida*, and *A. Lepigoni*, *Pythium*, *Plasmopara*, and *Sclerospora*, a single large central egg-cell or oosphere becomes differentiated in the protoplasm of the oogonium; this contains a single nucleus in a central position, while the remaining nuclei pass into the peripheral layer of protoplasm (periplasm). The antheridium now sends a process into the oogonium, which at its apex opens into the oosphere and allows a single male nucleus to pass into the latter (Fig. 321, 2). The oosphere then becomes surrounded with a cell wall (Fig. 321, 3), and nuclear fusion takes place, while the periplasm is utilised in forming the outer membrane of the spore (episporium). In *Peronospora parasitica* the ripe oospore has a single nucleus, in *Albugo* it becomes multinucleate as a result of nuclear division. In *Albugo Bliti* and *A. portulacae* there is also a central oosphere surrounded by periplasm, but the oosphere contains numerous nuclei, which fuse in pairs with a number of male nuclei entering from the antheridium. A multinucleate oospore thus arises from the compound egg-cell.

The behaviour of these two species can be regarded as primitive, the uninucleate oospheres of the first-named forms having been derived from the multinucleate condition. *Albugo tragopogonis* occupies an intermediate position in that its oosphere is at first multinucleate, but later contains only one female nucleus, the others having degenerated. The superfluous nuclei in the oogonia and antheridia may be regarded as the nuclei of gametes which have become functionless, and are comparable with the superfluous egg-nuclei of certain Fucaceae. The oospores either produce a mycelium directly or give rise to swarm-spores.

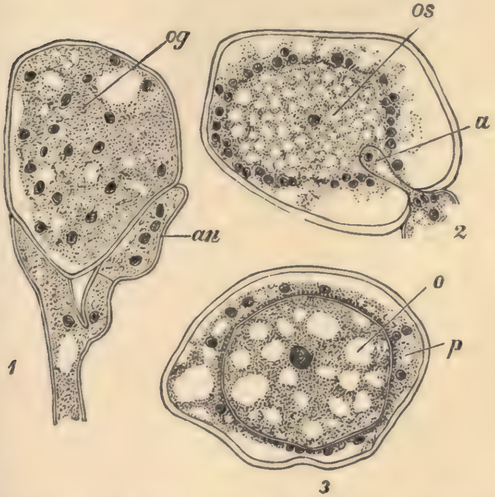


FIG. 321.—Fertilisation of the Peronosporeae. *1, Peronospora parasitica.* Young multinucleate oogonium (*og*) and antheridium (*an*). *2, Albugo candida.* Oogonium with the central uninucleate oosphere and the fertilising tube (*a*) of the antheridium which introduces the male nucleus. *3*, The same. Fertilised egg-cell (*o*) surrounded by the periplasm (*p*). (After WAGER. × 666.)

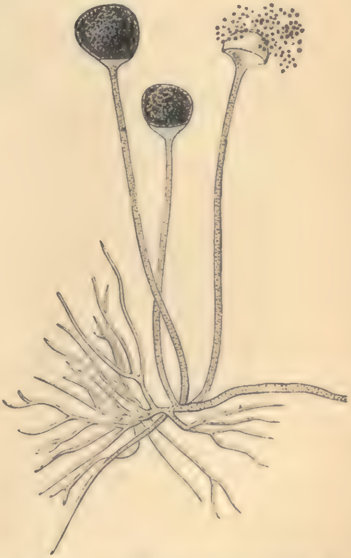


FIG. 322.—*Rhizopus nigricans* (= *Mucor stolonifer*). Portion of the mycelium with three sporangia; that to the right is shedding its spores and shows the persistent hemispherical columella. (× 38.)

Order 2. Zygomycetes

1. The **Mucorineae** (55) comprise a number of the most common Mould Fungi. They are saprophytic, and are found chiefly on decaying vegetable and animal substances. Asexual reproduction is effected by non-motile, walled spores, which either have the form of conidia or arise endogenously in sporangia. Sexual reproduction consists in the formation of zygospores, as a result of the conjugation of two equivalent cœnogametes.

One of the most widely distributed species is *Mucor Mucedo*, frequently found forming white fur-like growths of mould on damp bread, preserved fruits, dung, etc. *Mucor stolonifer* (= *Rhizopus nigricans*), with a brown mycelium, occurs on similar substrata. The spherical sporangia are borne on the ends of thick erect branches of the mycelium (Fig. 322). From the apex of each sporangiophore a single spherical sporangium is cut off by a transverse wall, which protrudes into the cavity of the sporangium and forms a columella (Fig. 323, 1, *c*). The contents of the sporangium become divided into numerous spores. These escape by the swelling of a substance which lies between the spores and the bursting of the sporangial wall. In *Pilobolus*, which occurs commonly on dung, the sporangium is forcibly cast off from the turgid sporangiophore which bursts at the columella.

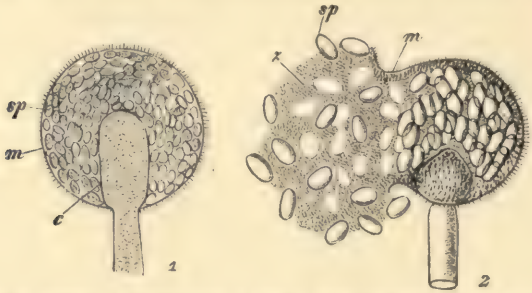


FIG. 323.—*1, Mucor Mucedo.* A sporangium in optical longitudinal section; *c*, columella; *m*, wall of sporangium; *sp*, spores. *2, Mucor mucilagineus.* A sporangium shedding its spores; the wall (*m*) is ruptured, and the mucilaginous substance between the spores (*x*) is greatly swollen. (After BREFELD, 1 × 225, 2 × 300, from v. TAVEL, *Pilze.*)

According to HARPER the spores of *Pilobolus* are binucleate, while those of *Sporodinia* (Fig. 324) are multinucleate.

Under certain conditions, instead of asexual sporangia, organs of sexual reproduction are produced. The hyphæ of the mycelium then give rise to lateral, club-shaped branches. When the tips of two such branches come into contact, a conjugating cell or cœnogamete is cut off from each by a transverse wall (Fig. 325). The two gametes thereupon coalesce, their nuclei conjugating in pairs, and fuse into a ZYGOSPORE, the outer wall of which is covered with warty protuberances. After a period of rest the zygospore germinates, developing a germ-tube, which may at once bear a sporangium (Fig. 325, 5).

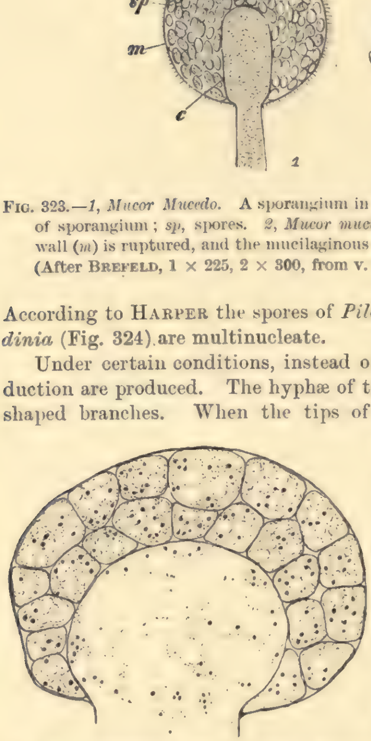


FIG. 324.—*Sporodinia grandis.* Median section of a ripe sporangium. The spores are multinucleate. (After HARPER, × 425.)

BLAKESLEE'S (56) demonstration of the diœcious nature of the mycelium of *Mucor stolonifer* is of great interest. The formation of zygospores only takes place when male and female mycelia come in contact. In other Mucorineae the two conjugating gametes may arise on the same mycelium.

Within the group of the Zygomycetes a reduction of sexuality is perceptible. Thus, in the case of certain Mucorineae, although the conjugating hyphæ meet in pairs, no fusion takes place, and their terminal cells become converted directly into spores, which are termed AZYGOSPORES. In other forms again, hyphæ producing azygospores are developed, but remain solitary, and do not, as in the preceding case, come into contact with similar hyphæ. There are also many species in which the formation of zygospores is infrequent.

Both the size and number of spores produced in the sporangia of *Mucor Mucedo* are subject to variation. The sporangia of the genus *Thamnidium* are, on the other hand, regularly dimorphic, and a large sporangium containing many spores is formed at the end of the main axis of the sporangiophore, while numerous small sporangia, having but few spores (sporangioles), are produced by its verticillately branching lateral axes. The sporangia may at times develop only a single spore, as the result of certain conditions of food-supply, and in this way assume the character of conidia. This dimorphism is even more complete in the tropical genus *Choanephora*. In this case, in addition to large sporangia, conidia are produced on special conidiophores. There are, finally, Zygomycetes (*e.g. Chaetocladium*) whose only asexual spores are conidia. In this one group, therefore, all transitional forms, from many-spored sporangia to unicellular conidia, are represented.

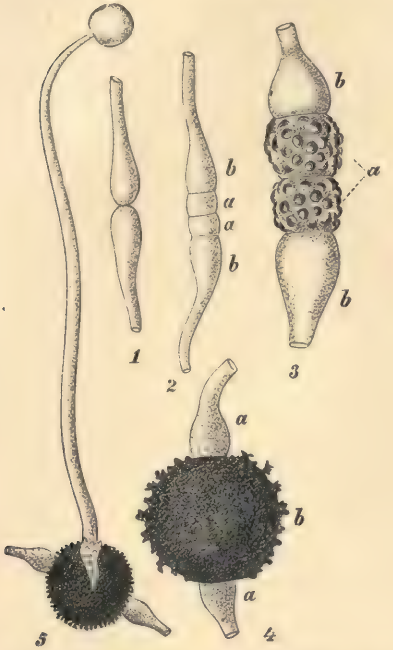


FIG. 325.—*Mucor Mucedo.* Different stages in the formation and germination of the zygospore. *1*, Two conjugating branches in contact; *2*, septation of the conjugating cells (*a*) from the suspensors (*b*); *3*, more advanced stage, the conjugating cells (*a*) are still distinct from one another: the warty thickenings of their walls have commenced to form; *4*, ripe zygospore (*b*) between the suspensors (*a*); *5*, germinating zygospore with a germ-tube bearing a sporangium. (After BREFELD, 1-4 × 225, 5 × circa 60, from v. TAVEL, *Pilze*.)

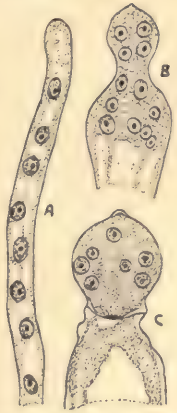


FIG. 326.—*Empusa Muscae.* *A*, Hypha from the body of a fly. *B*, Young conidiophore arising from the mycelium and projecting from the body of the insect. *C*, Formation of the conidium into which the numerous nuclei have passed from the conidiophore. (After OLIVE, × 540.)

2. The **Entomophthorineae** (57) is a small group of Fungi which mostly live parasitically in the bodies of insects and caterpillars. The multinucleate mycelium remains non-septate or later becomes divided into cells. Asexual multiplication is effected by means of conidia which contain one or numerous nuclei. These arise singly at the ends of branches of the mycelium and when ripe are forcibly abjected. Sexual reproduction is by means of zygospores, in place of which azygospores frequently arise.

The best-known example is *Empusa muscae* (Fig. 326), which is parasitic on house-flies. The conidia, which are multinucleate, form a white halo around the body of the dead fly which has been killed by the fungus.

3. **Basidiobolaceae** (58).—*Basidiobolus ranarum*, a saprophytic Fungus growing on the excrement of Frogs, must be separated from the preceding group. Each of the cells of its septate mycelium contains one large nucleus. The conidia which arise singly on the ends of the conidiophores and are abjected when ripe are uninucleate. The mode of origin of the zygospores is peculiar. Two adjoining cells conjugate after they have put out beak-shaped processes which are cut off as transitory cells. In the zygospore the two sexual nuclei give rise to four, of which two disorganise while the other two fuse. Both in this procedure and in the nuclear structure there are evident resemblances to the Conjugatae (*Spirogyra*).

Class XIV

Eumycetes (48, 49)

When the Phycomycetes are excluded there remain two great groups of Fungi, the Ascomycetes and the Basidiomycetes, regarding the classification and phylogeny of which there is still much uncertainty. The attempt has been made to derive them from the Phycomycetes. Not only is the construction of the thallus against this, but the structure of the sexual organs and the development of the fruit in the Ascomycetes indicate on the other hand a remarkable relationship with the Red Algae. The Uredineae or Rusts, one of the simplest orders of Basidiomycetes, appear to connect the latter group with the Ascomycetes.

The saprophytic or parasitic thallus of the Eumycetes is, like that of the Phycomycetes, composed of fine, richly branched filaments or hyphæ which together form the mycelium. The hyphæ are, however, in this case septate, consisting of rows of cells. The cell-membrane, which contains chitin, is usually thin. In the colourless protoplasm there are usually numerous minute nuclei (Fig. 62), while in other cases each cell has a pair of nuclei or only a single nucleus. Chromatophores are wanting and true starch is never formed; the place of the latter is taken by glycogen, often in considerable quantity, and by fat-globules. The hyphæ of a mycelium are, as a rule, either isolated or only loosely interwoven; they spread through the substratum in all directions in their search for organic nourishment. In many of the higher Fungi, however, the profusely branching hyphæ form compact masses of tissue. Where the filaments in such cases are in intimate contact and divided into short cells, an apparently parenchymatous tissue or PSEUDO-PARENCHYMA is produced. Such compact masses of hyphal tissue are formed by some species of Fungi when their mycelia, in passing into a vegetative resting stage, become converted into SCLEROTIA, tuberous or strand-like, firm, pseudo-parenchymatous bodies, which germinate under certain conditions (Fig. 107). In the fructifications the hyphæ are also nearly always aggregated into a more or less compact tissue (Fig. 106).

The distinction between the two main groups is apparent in their reproductive organs.

1. The **Ascomycetes** in their typical forms possess sexual organs. The oogonia, which here go by the name of ascogonia or, as in the Red Algae, of carpogonia, show profound differences in the genera which have as yet been accurately investigated and the same may be said of the male organs. In all cases, however, the fertilised carpogonium does not become a resting oospore, but, while in connection with the maternal plant (gametophyte), develops into an asexual generation (sporophyte). In this process hyphæ bud out from the carpogonium, and their ultimate branches terminate in the asci which are sporangia of a specialised type.

The ASCUS (60), which is so characteristic of the whole group, originates from a tubular cell; this to start with contains two nuclei which fuse, and the resulting nucleus by repeated division gives rise to eight nuclei. By a process of free cell-formation the spores become limited by cell-walls in the way shown in Fig. 96 (Figs. 327, 334). In contrast to the formation of spores in the sporangia of Phycomycetes the cytoplasm of the ascus is not completely used up in the formation of the ascospores. The spores usually form a longitudinal row, and are ultimately ejected from the ruptured apex of the ascus by the swelling of the remaining cytoplasm. In the great majority of the Ascomycetes the number of ascospores in the ascus is eight.

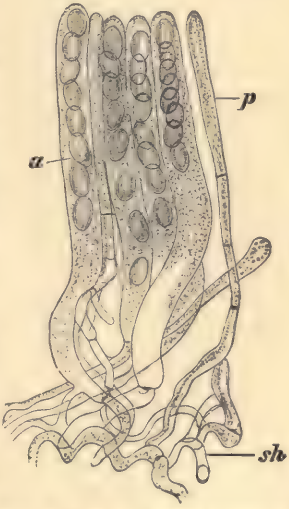


FIG. 327.—Portion of the hymenium of *Morchella esculenta*. *a*, Asci; *p*, paraphyses; *sh*, subhymenial tissue. (× 240.)

In the majority of Ascomycetes the asci, which originate from the carpogonium, are associated in special fructifications; vegetative filaments of the mycelium take part in the formation of these.

Sexual organs are not at present known in all the groups of Ascomycetes. In certain orders they are entirely wanting, perhaps as a result of reduction, so that the asci in these cases spring directly from the mycelium.

2. The **Basidiomycetes** no longer possess sexual organs; only in the Uredineae or Rust-fungi are structures found which can be regarded as persisting male organs, and cells which appear to correspond to the carpogonia of Ascomycetes (cf. p. 406). Asci are

not developed in Basidiomycetes, which are characterised by a special kind of spore, the basidiospores. These are produced by a process of budding on the characteristic BASIDIA, each of which bears a definite number of spores, usually four. The typical basidia (Figs. 343, 344) are either terminal tubular cells bearing the four spores at their upper ends, or they are four-celled, each cell giving rise to a spore. The spores are borne on thin stalk-like sterigmata, from which they become separated when mature. The basidia agree with the asci in containing when young two nuclei, which fuse with one another. The resulting nucleus then divides into the nuclei for the four spores (71).

In most Basidiomycetes the basidia are borne on or in special fructifications, the origin of which is not, however, dependent on a sexual process.

The general name of CONIDIA is given to fungal spores which arise by a process of budding, and the simple or branched hyphæ bearing them are termed conidiophores. The basidia are thus a special form of the latter, but are distinguished from other conidiophores by their peculiar nuclear fusion.

Other forms of conidiophore in addition to the basidia occur in the life-history of some Basidiomycetes. In the Ascomycetes also the formation of conidia as well as asci is a widespread method of asexual reproduction. In general, it may be said that the asexual formation of spores in the Fungi takes place in a large number of different ways.

The direct origin of spores from the cells of a hypha which round off, become thick-walled and ultimately separate from one another (chlamydospores of Brefeld), must be distinguished from the formation of conidia. The spores of the Ustilagineae are thus formed in rows, while the uredo-spores of the Uredineae arise at the ends of hyphæ.

All the asexual spores of the Eumycetes are provided with cell walls, and are adapted for distribution through the air.

Sub-Class I. Ascomycetes (48, 49, 59, 60)

The sexual organs have been accurately investigated in relatively few forms; a number of distinct types are found.

1. In the Laboulbeniaceae (Fig. 342) the carpogonium with its trichogyne, and the antheridia which produce spermatia, show a striking correspondence with the structures of the same name in the Red Algae.

2. The Ascomycetes which enter into the composition of Lichens (Figs. 372, 373) approach most closely the preceding group. The carpogonium is here a spirally wound filament of cells terminating in a trichogyne. The spermatia are formed in special flask-shaped depressions of the thallus, the spermogonia. Similar reproductive

organs occur in some Ascomycetes (*e.g. Polystigma*) which do not form parts of Lichens.

3. *Pyronema* (Fig. 333) and related genera together with *Boudiera* (62) exhibit a quite distinct type. A multinucleate carpogonium which is provided with a trichogyne is fertilised by a multinucleate antheridium, the two structures being thus coenogametes.

4. In the Erysipheae (Fig. 328) a uninucleate antheridium unites directly with a uninucleate oogonium.

It remains for future research to determine whether these types are to be derived from a single one or whether they indicate a polyphyletic origin for the Ascomycetes.

In many genera the sexual organs are more or less reduced, and in some groups of Ascomycetes they are completely wanting.

Ascogenous filaments which bear the asci on their ultimate ramifications (cf. Fig. 334) arise from the carpogonium. Sterile hyphæ which arise from below the carpogonium also take part in the formation of the fructification, forming an investment to it and paraphyses standing between the asci. The two sorts of hypha are, however, clearly distinguishable.

The orders of Ascomycetes are provisionally characterised by the construction of the fructification.

In the Perisporiaceae the small, spherical fruits (perithecia) are surrounded by a complete investing layer, on the rupture or rotting of which the spores are set free.

In the Discomycetes open cup-, club-, or hat-shaped fructifications (apothecia) are formed; the asci are arranged parallel to one another in a superficial layer termed the hymenium.

In the Pyrenomycetes the perithecia are flask-shaped, the asci springing from the base of the cavity.

In the Tuberaceae the subterranean, tuberous fructifications are closed.

To these orders must be added the Exoasci, in which the asci arise from cells of the mycelium without the formation of any fructification, and the very simple Saccharomycetes or Yeast-Fungi. These two groups can be regarded as extremely reduced Ascomycetes.

The Laboulbeniaceae in which the asci are enclosed in small perithecia occupy an isolated position.

Order 1. Perisporiaceae (48, 61)

This order, which includes only Ascomycetes with enclosed fructifications, comprises two families: the Erysipheae or Mildew Fungi and the Perisporieae.

1. The **Erysipheae** form a family of distinctive, epiphytic parasites whose mycelium, somewhat resembling a cobweb, and ramifying in all directions over the surface, particularly the leaves, of higher plants, sends out haustoria which penetrate the epidermis of the host. In some cases the mycelium also inhabits

the intercellular spaces of the leaf. The ripe ascus fructifications (perithecia) are small black bodies provided with peculiar appendages. In the simplest forms (*e.g.* in the genus *Sphaerotheca*) the spheroid perithecium encloses only a single ascus with eight spores. It is enveloped by a covering of sterile hyphæ, forming a sheathing layer, two to three cells deep. The genera *Erysiphe* and *Uncinula*, on the other hand, develop in each perithecium several asci, and in *Phyllactinia* 12 to 25 asci are present. Since all the eight nuclei are not utilised in spore formation the number of spores in each ascus is usually 4 or only 2. The perithecia are irregularly ruptured at their apices and the spores are thus set free. As HARPER has shown, the first rudiment of the perithecium consists of an oogonium and an antheridium. These are uninucleate cells, separated from the mycelium by partition walls, and stand close together. The male nucleus passes into the oogonium by an opening which forms in the cell walls (Fig. 328, 1-4). After fertilisation the oogonium is surrounded by investing filaments which spring from its stalk-cell or from that of the antheridium (5), and the oogonium itself becomes converted into a multicellular structure (6). In *Sphaerotheca* the ascus containing eight spores arises from the multinucleate terminal cell, while in *Erysiphe* and *Phyllactinia* this cell produces ascogenous hyphæ which in turn give rise to the numerous asci.

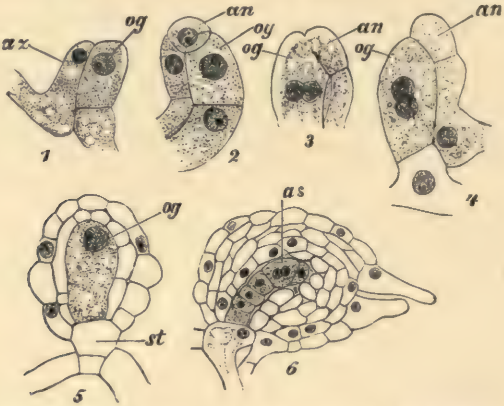


FIG. 328.—*Sphaerotheca castagnei.* Fertilisation and development of the perithecium. *1*, Oogonium (*og*) with the antheridial branch (*az*) applied to its surface; *2*, separation of antheridium (*an*); *3*, passage of the antheridial nucleus towards that of the oogonium; *4*, union of the nuclei; *5*, fertilised oogonium surrounded by two layers of hyphæ derived from the stalk-cell (*st*); *6*, the multicellular ascogonium derived by division from the oogonium; the terminal cell with the two nuclei (*as*) gives rise to the ascus. (After HARPER.)

Before entering upon the formation of perithecia, the Mildew Fungi multiply by means of conidia abstricted in chains from special, erect hyphæ, from the tip downwards. The Mildew Fungus of the Grape-vine occurs on the leaves and berries in America and has appeared in Europe since 1845. This fungus, known as *Oidium Tuckeri*, is the conidial form of *Uncinula necator* (= *U. spiralis*), the small perithecia of which have appendages spirally rolled at their free ends and are only rarely found (Fig. 329).

2. The **Perisporieae** are closely related to the Erysipheae, but are saprophytic and live on decomposing organic matter. To this order belong two of the most

common Mould Fungi, *Aspergillus* (*Eurotium*), *herbariorum* and *Penicillium crustaceum.* Both multiply extensively by means of conidia before they begin to form perithecia.

In the case of *Aspergillus herbariorum*, the conidia are abstricted in chains from a number of sterigmata arranged radially on the spherical, swollen ends of the conidiophores (Fig. 330). The conidiophores are closely crowded together, and constitute a white mould, afterwards turning to a blue-green, frequently found on damp vegetables, fruit, bread, etc. Some species of *Aspergillus* are pathogenic in man and other mammals; thus *A. fumigatus* causes mycosis of the external ear, the throat, and the lungs.

In *Penicillium crustaceum*, another widespread blue-green mould, the erect conidiophores (Fig. 330) are verticillately branched. The spherical perithecia of *Aspergillus* and *Penicillium* are produced later on the mycelium, but only rarely occur in the latter genus. Their structure is more complicated than in the Erysipheae. They originate as a spirally wound carpogonium which after fertilisation becomes surrounded by lateral branches of the mycelium. The ascogenous hypha branches, penetrating the pseudo-parenchymatous tissue within the perithecium, and bears numerous round asci containing eight spores. The walls of the asci and the surrounding pseudo-parenchyma disappear in the ripe fructification which opens irregularly by the rupture of the peripheral layer.

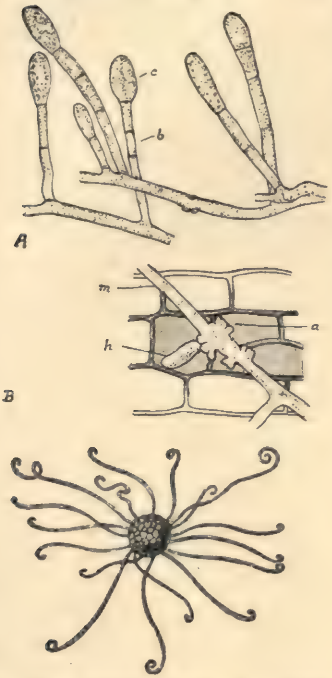


FIG. 329.—*Uncinula necator.* *A*, Conidial stage ; *c*, conidium ; *b*, conidiophore. *B*, Hypha which has formed a disc of attachment (*a*) and has sent a haustorium (*h*) into an epidermal cell. *C*, Perithecium with appendages. (From SORAUER, LINDAU, and REH. *Handb. d. Pflanzenkrankheiten*, ii. p. 194. 1906.)

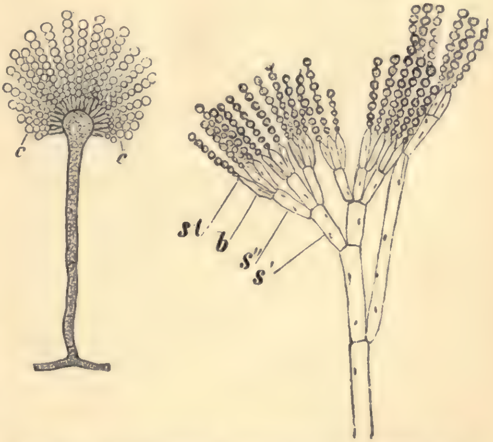


FIG. 330.—Conidiophores of *Aspergillus herbariorum* (to the left) and *Penicillium crustaceum* (to the right.)

Order 2. Discomycetes (48, 62)

The Discomycetes are distinguished from the other orders by their open apothecia, which bear the hymenium, consisting of asci and paraphyses, freely exposed on their upper surface (Fig. 332). The different groups exhibit great diversity as regards the manner of development of their fructifications.

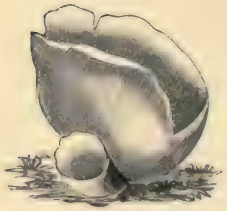


FIG. 331.—*Peziza aurantiaca.* (After KROMBHOLZ, nat. size.)

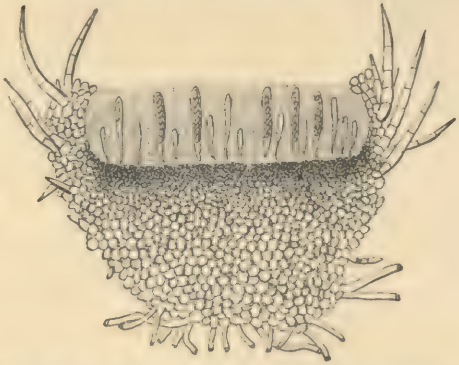


FIG. 332.—*Lachnea pulcherrima.* Apothecium ruptured, showing old and young asci between the paraphyses. (After WORONIN, from v. TAVEL.)

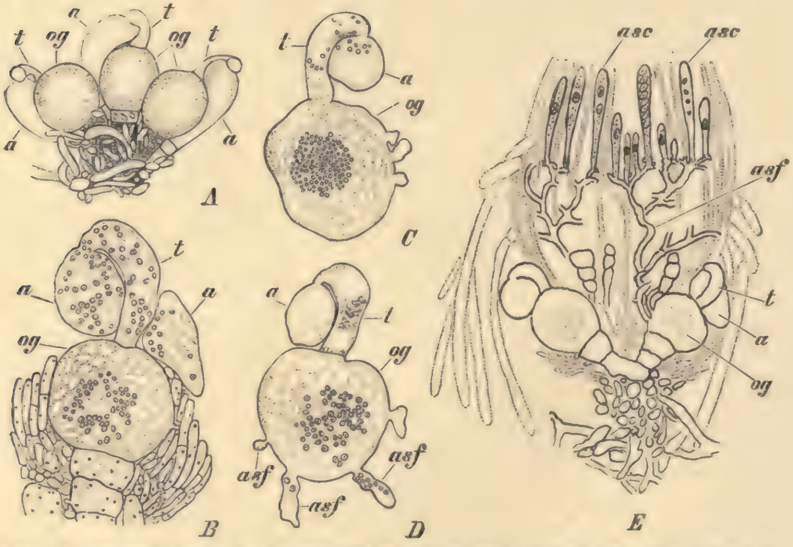


FIG. 333.—*Pyronema confluens.* *A*, Rudiment of an apothecium, consisting of three oogonia (*og*), with trichogynes (*t*) and three antheridia (*a*). *B*, Fusion of the antheridium and the tip of the trichogyne. *C*, The basal-wall of the trichogyne having been absorbed, the male and female nuclei are grouped in the centre of the oogonium. *D*, Separation of the oogonium from the trichogyne by means of a new partition wall. Formation of the ascogenous filaments (*asf*). *E*, Longitudinal section through a young apothecium. *asc*, Asci. (After R. HARPER. *A*, *E* × about 150, *B*-*D* × about 300.)

The great majority of the Discomycetes, of which the genus *Peziza* may serve as a type, grow on living or dead vegetable substances, especially upon decaying wood, but sometimes also on humus soil. They produce saucer- or cup-shaped fructifications of a fleshy or leathery consistency, and usually of small dimensions. One of the largest forms, *Peziza aurantiaca* (Fig. 331), has irregularly bowl-shaped fructifications, which may be seven centimetres broad and of a bright orange-red colour, while in most of the other species they are grey or brown. Such cup-shaped fructifications are termed APOTHECIA.

The development of the apothecium may be described for *Pyronema confluens*, in which it has been thoroughly investigated by R. HARPER. The fruit-body of this species is about 1 mm. across, and of a yellow or reddish colour; it often occurs on spots where fires have been kindled in woods. The carpogonia are especially large in this species, and several usually take part in the formation of each apothecium (Fig. 333 *A*). The carpogonium or ascogonium consists of the spherical, multinucleate oogonium, on the apex of which a multinucleate curved cell, the trichogyne, is situated. The cylindrical, multinucleate antheridium arises below the oogonium; its apex comes into open communication with the tip of the trichogyne by the breaking down of the intervening walls. The male nuclei first wander into the trichogyne cell, and then, by the breaking down of the basal wall of the latter, into the oogonium. In the oogonium the male nuclei conjugate in pairs with the numerous female nuclei, while the nuclei of the trichogyne cell disintegrate. The egg-cell then becomes limited from the trichogyne by a new cell wall and sends out ascogenous filaments containing the conjugated nuclei. These filaments branch and ultimately terminate in asci (*E*), while the sterile hyphæ and the paraphyses of the fructification are derived from hyphæ arising beneath the carpogonium. In *Ascobolus*, a genus related to *Pyronema*, the ascogonium is to begin with multicellular, but all the cells empty their contents into a single large one, from which the ascogenous hyphæ then arise.

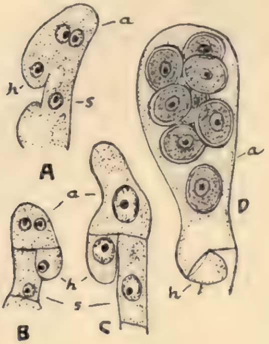


FIG. 334.—Development of the Ascus. *A-C*, *Pyronema confluens*. (After HARPER.) *D*, Young ascus of *Boudiera* with eight spores. (After CLAUSSEN.) Explanation in text.

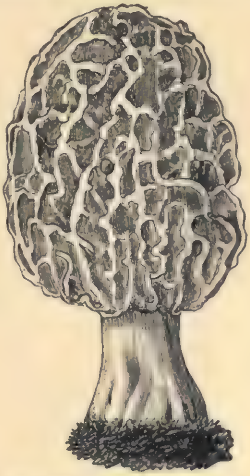


FIG. 335.—*Morchella esculenta*. (½ nat. size.)

The end of the ascogenous hypha (^{60}) when about to form an ascus becomes curved into a hook-like shape (Fig. 334 *A*). The two nuclei of the young ascus (*a*) lie near to the bend, and on the formation of transverse walls are separated from the uninucleate terminal cell (*h*) and the stalk-cell (*s*) which also has a single nucleus. The two nuclei of the young ascus fuse (*C*), and the resulting nucleus gives rise by repeated division to the nuclei of the eight ascospores (*D*).

The highest development is exhibited by the peculiar fructifications of the Helvellaceae, whose mycelium grows in the humus soil of woods. In the genus *Morchella* (Fig. 335), the fructifications consist of a thick erect stalk, bearing a club-shaped or more or less spherical cap or pileus, which bears the hymenium, with its eight-spored asci, on the reticulately indented exterior surface (Fig. 327). The Morchellas are edible (63), in particular *M. esculenta* and *M. conica*. The former has a yellowish-brown cap, ovately spherical in shape, and attains a height of 12 cm.; the cap of the latter is conical and dark brown, and it reaches a height of 15 cm. *Gyromitra esculenta*, with dark brown cap and white stalk, and others are also edible. In their external appearance the fructifications of these highly developed Discomycetes greatly resemble those of the Basidiomycetes.

Order 3. Pyrenomycetes (48, 49)

The Pyrenomycetes comprise an exceedingly varied group of Fungi, some of which are parasitic upon different portions of plants, particularly on the cortex and leaves, and others are saprophytic upon decaying wood, dung, etc., while a few genera occur as parasites upon the larvæ of insects. The flask-shaped fructifications or perithecia are characteristic of this order. The perithecia are open at the top, and are covered inside, at the base, with a hymenial layer of asci and hair-like paraphyses (Fig. 336). The lateral walls are coated with similar hyphal hairs, the periphyses. The ascospores escape from the perithecia through the aperture. In this process one ascus after another elongates in consequence of the water absorbed, and ejects its spores through the opening, or the spores are set free within the perithecia, and are pressed out, embedded in a swollen mass of mucilage.

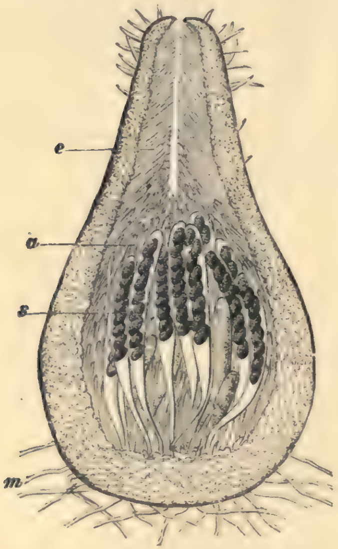


FIG. 336.—Perithecium of *Podospora fimiseda* in longitudinal section. *s*, Asci; *a*, paraphyses; *e*, periphyses; *m*, mycelial hyphæ. (After v. TAVEL, × 90.)

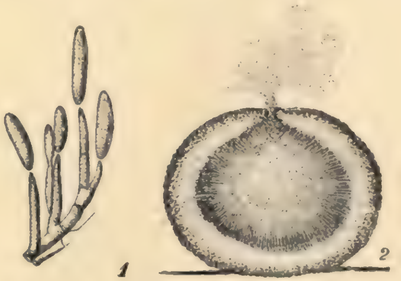


FIG. 337.—*1*, Conidiophore abstricting conidia, from a pycnidium of *Cryptospora hypodermia*. (After BREFELD, × 300.) *2*, Pycnidium of *Strickeria obducens* in vertical section. (After TULASNE, × 70.)

The simplest Pyrenomycetes possess free perithecia (Fig. 336) which are usually small and of a dark colour, and grow singly on the inconspicuous mycelium (*e.g. Nectria*, *Sphaeria*, and *Podospora*). In other cases the perithecia are in groups embedded in a cushion- or club-shaped, sometimes branching, mass of compact mycelial hyphæ having a pseudo-parenchymatous structure. Such a fructification is known as a STROMA.

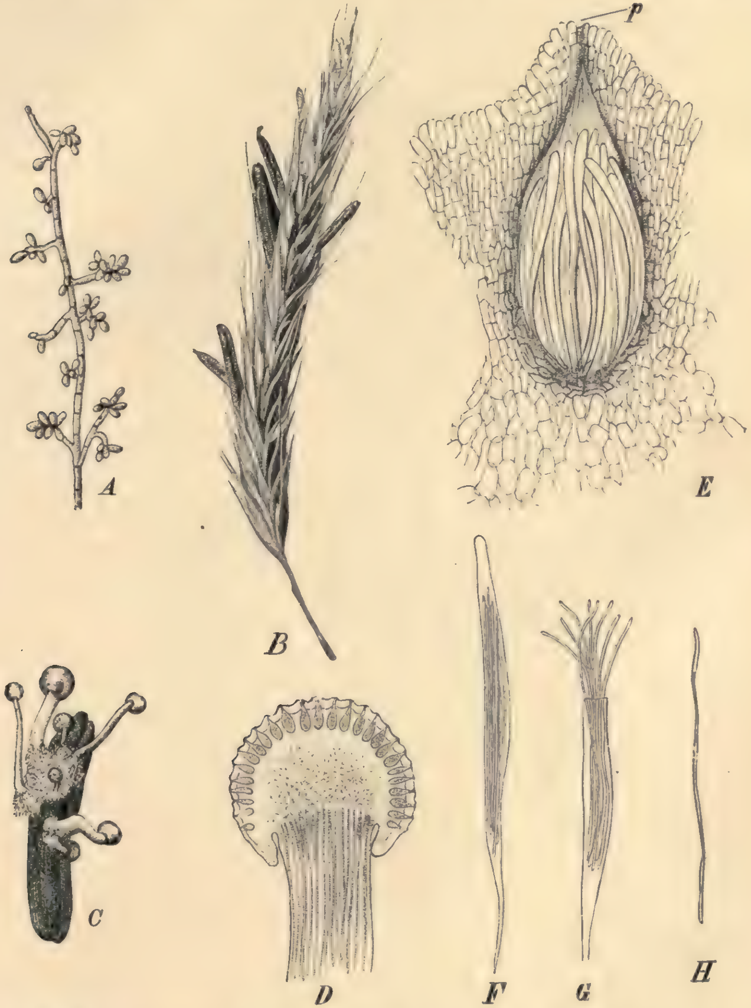


FIG. 338.—*Claviceps purpurea*. *A*, Mycelial hypha with conidia; *B*, ear of Rye with several ripe sclerotia; *C*, a sclerotium with stromata; *D*, longitudinal section of a fructification showing numerous perithecia; *E*, a single perithecium, more highly magnified; *F*, ascus with eight filiform spores; *G*, a ruptured ascus with escaping spores; *H*, a single spore. (*A* after BREFELD; *C-H* after TULASNE; *B* photographed from nature. OFFICIAL and POISONOUS.)

In the life-history of most Pyrenomycetes the formation of perithecia is preceded by the production of various accessory fructifications, particularly of conidia, which are abstricted in different ways, either directly from the hyphæ or from special conidiophores, and assist in disseminating the fungus. The conidiophores are frequently united in distinct, conidial fructifications. A special form of such fructifications are the PYCNIDIA produced by many genera. They are small spherical or flask-shaped bodies which give rise to branched hyphal filaments from the apices of which conidia, in this case termed PYCNOSPORES or PYCNOCONIDIA, are abstricted (Fig. 337, 1, 2). The structure of the pycnidia and

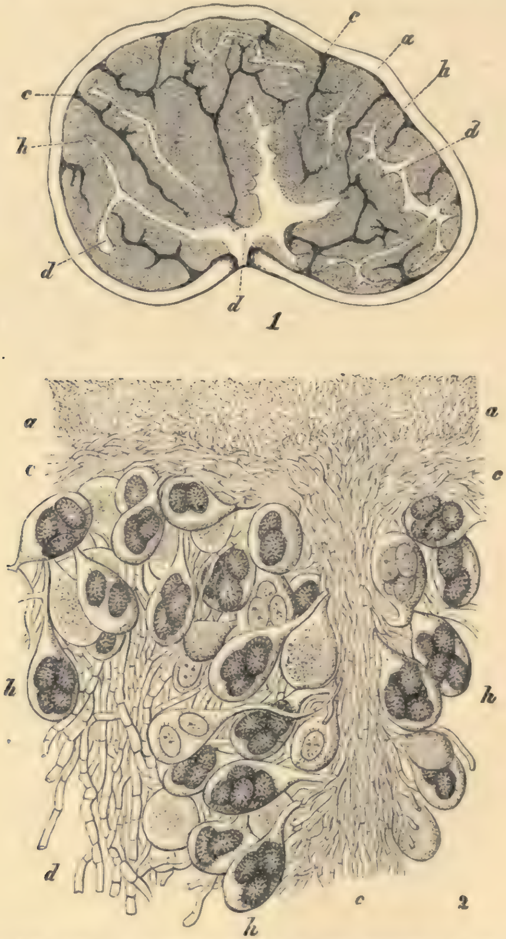


FIG. 339.—*Tuber rufum.* *1*, A fructification in vertical section (× 5); *a*, the cortex; *d*, air-containing tissue; *c*, dark veins of compact hyphæ; *h*, ascogenous tissue; *2*, a portion of the hymenium (× 460). (After TULASNE, from V. TAVEL.)

pycnospores corresponds to that of the spermogonia and spermatia of the Lichens, and they may in part at least be regarded as male organs.

Claviceps purpurea, the fungus of Ergot, is important on account of its official value. It is parasitic in the young ovaries of different members of the Gramineae, particularly of Rye. The ovaries are infected in early summer by the ascospores. The mycelium soon begins to form conidia, which are abstricted in small clusters from short lateral conidiophores (Fig. 338 *A*). At the same time a sweet fluid is extruded. This so-called HONEY-DEW is eagerly sought by insects, and the conidia embedded in it are thus carried to the ovaries of other plants. The conidial form of this Fungus was formerly regarded as a distinct genus under the name of *Sphacelia segetum*. After the completion of this form of fructification, and the absorption of the tissue of the ovary by the mycelium, a sclerotium is eventually formed in the place of the ovary from the hyphæ of the mycelium by their intimate union, especially at the periphery, into a compact mass of pseudo-parenchyma (Fig. 107). These elongated dark-violet SCLEROTIA, which project in the form of slightly curved bodies from the ears of corn, are known as Ergot (Fig. 338, *B*). The sclerotia, copiously supplied with reserve material (fat), eventually fall to the ground, where they pass the winter, and germinate in the following spring when the Rye is again in flower. They give rise to bundles of hyphæ which produce long, stalked, rose-coloured globular heads (*C*). Over the surface of the latter are distributed numerous sunk perithecia (*D*, *E*). Each perithecium contains a number of asci with eight long, filiform ascospores, which are ejected and carried by the wind to the inflorescences of the grass.

Nectria ditissima (64) is a very injurious parasitic fungus which inhabits the cortex of various trees and causes the canker of fruit trees. It is propagated in summer by means of slightly curved, fusiform, multicellular conidia, and in winter and spring forms small red perithecia which are closely crowded together.

OFFICIAL.—Ergot is the sclerotium of *Claviceps purpurea*.

Order 4. Tuberaceae (Truffles) (65)

The Tuberaceae or Truffle Fungi are saprophytic Ascomycetes whose mycelium occurs in humus soil, particularly in woods. The ascus fructifications familiar under the name of truffles are underground tuberous bodies (Fig. 339), consisting of a thick, investing layer, enclosing an inner mass in which the club-shaped asci occur (Fig. 339, 2). The asci contain only a small number of spores ; in the case of the true truffles (*Tuber*) they are usually only four in number, and generally have a spinous or reticulately thickened epispore. When the fructifications are fully mature, the ripe spores lie free within the fructification.

The fructifications of many of the Tuberaceae are edible (63), and have an aromatic odour and taste. They are, for the most part, obtained from France and Italy. Of the edible varieties, the most important are the so-called black truffles belonging to the genus *Tuber*, viz. *Tuber brumale*, *melanosporum*, *aestivum*, *mesentericum*. The fructifications of these species have a warty cortex of a black, reddish-brown, or dark brown colour. The white truffle, *Choiromyces meandriformis*, the external surface of which is pale brown, is also edible.

Elaphomyces granulatus (*Boletus cervinus*), the yellowish-brown fructifications of which are of the size of a walnut and have a bitter taste, occurs commonly in woods in Europe. It is used in veterinary medicine.

Order 5. Exoasci (66)

The most important genus of this group of Ascomycetes is *Taphrina* (including *Exoascus*), the species of which are parasitic on various trees. They develop in part annually beneath the cuticle of the leaves, causing discolorations of these organs; their mycelium persists during the winter in the tissue of the host, so that a constant recurrence of the disease takes place. The presence of the mycelium in the tissues of the infected part causes the abnormally profuse development of branches known as WITCHES'-BROOMS. *Taphrina Carpini* produces the abnormal growths occurring on the Hornbeam; *Taphrina epiphylla*, those of *Alnus incana*. *Taphrina deformans* attacks the leaves of the Peach and causes them to curl. *Taphrina Pruni* is parasitic in the young ovaries of many species of *Prunus*, and produces the malformation of the fruit known as "Bladder Plums," containing a cavity, the so-called "pocket," in the place of the stone; the mycelium persists through the winter in the branches. In the formation of asci, which occurs without the formation of sexual organs, individual cells of the copiously-branched mycelium ramifying between the epidermis and cuticle of the infected part become greatly swollen. These grow into club-shaped tubes, which burst through the cuticle and, after cutting off a basal stalk-cell, are usually converted into asci with eight spores (Fig. 340). The numerous asci are closely crowded together. In consequence of their increased turgor, resulting from an excessive absorption of water, the asci become ruptured at their free extremities and eject the spores.

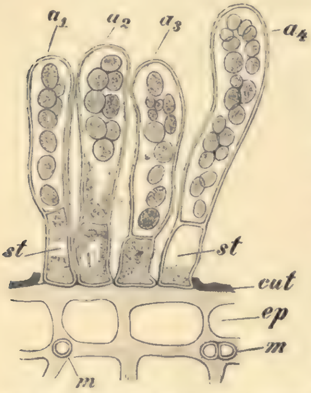


FIG. 340.—*Taphrina Pruni*. Transverse section through the epidermis of an infected plum. Four ripe asci, a_1, a_2 with eight spores, a_3, a_4 with yeast-like conidia abstricted from the spores; *st*, stalk-cells of the asci; *m*, filaments of the mycelium cut transversely; *cut*, cuticle; *ep*, epidermis. (After SADEBECK, × 600.)

The spores, which bud in water or sugar solution, frequently germinate while still enclosed within the asci (Fig. 340, a_3, a_4), and give rise by budding to yeast-like conidia, *e.g.* in *Taphrina Pruni*.

The Exoasci are perhaps to be regarded as reduced Ascomycetes, in which the sexual organs have become completely suppressed.

Order 6. Saccharomycetes (Yeast-Fungi) (67)

The beer, alcohol, and wine yeasts included in the genus *Saccharomyces* are simple unicellular Fungi which assume the form of spherical, oval, or cylindrical conidia containing a single nucleus. They increase in number by budding (Fig. 341). No mycelium is formed, though sometimes the cells remain for a time united in chains. With free access of oxygen and at a suitable temperature yeasts form asci when the nutrient substratum is exhausted; the asci externally resemble the conidia but contain a few spores. In some yeasts a conjugation of two cells accompanied by a nuclear fusion has been observed (68). In *Saccharomyces Ludwigii* the four spores in the ascus germinate and fuse in pairs by means of a narrow conjugation-tube; the latter elongates into a germ-tube from which yeast-cells are abstricted. In the ginger-beer yeast (*Zygosaccharomyces*) and in *Schizosaccharomyces* the yeast-cells conjugate by means of long tubes before spore-formation. These nuclear fusions possibly correspond to those in the young asci of other Ascomycetes.

Physiologically these Fungi are remarkable for their power of exciting, by means of an enzyme (zymase), the fermentation of saccharine solutions, alcohol and carbon dioxide being produced. The beer yeast (*Saccharomyces cerevisiae*) is only known in the cultivated form; the wine yeast (*S. ellipsoideus*), on the other hand, occurs regularly in the soil of vineyards in the spore-form; the latter is therefore always present on the grapes and need not be added to the grape-juice. Other genera, in some of which a mycelium is developed, belong to this order.

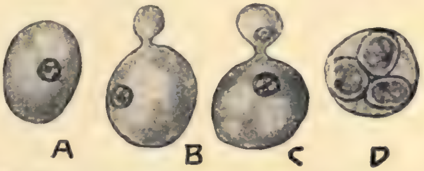


FIG. 341.—*Saccharomyces cerevisiae*. *A*, yeast-cell; *B*, *C*, yeast-cell budding; *D*, ascus with four spores. (After GUILLIERMOND, × 1125.)

No evidence is at present forthcoming to show that the Yeasts are to be regarded as developmental forms of other Fungi. In various members of the Exoasci, and Ustilagineae, however, yeast-like conidia which reproduce by budding are known. Possibly the Saccharomycetes are reduced Ascomycetes, or they may represent an independent group of very simple Fungi.

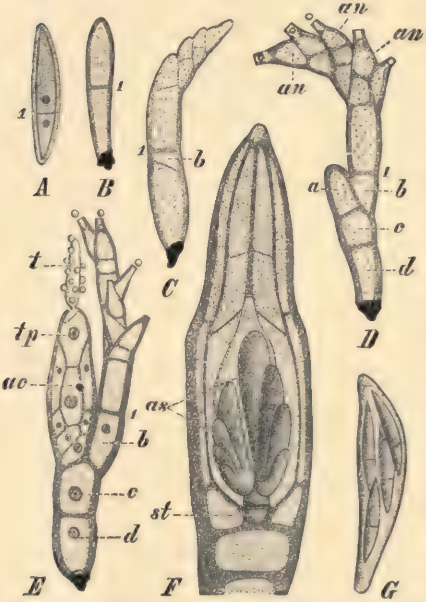


FIG. 342.—*Stigmatomyces Baeri*. Description in text. *A*, spore; *B-F*, successive developmental stages. *D*, with spermatia escaping from the antheridia *an*; *E*, with antheridia above and the lateral female organ; *F*, Perithecium with developing asci; *G*, ripe ascus. (After THAXTER.)

Order 7. Laboulbeniaceae (⁶⁹)

The Laboulbeniaceae are a group of minute Fungi occupying an isolated position; our knowledge of them is largely due to the work of THAXTER. Their thallus consists of two to a number of cells, and is attached to the body of the insect, most commonly a beetle, on which it is parasitic by means of a pointed process of the lowest cell inserted into the chitinous integument of the insect or by means of rhizoids which penetrate more deeply. *Stigmatomyces Baeri* which occurs on house-flies in Europe may be taken as an example. The bicellular spore (Fig. 342 *A*), which has a mucilaginous outer coat, becomes attached by its lower end (*B*), and divisions occur in both cells (*C*). From the upper cell an appendage is developed bearing a number of unicellular, flask-shaped antheridia (*D*, *an*) from which naked spherical spermatia without cilia are shed. The lower cell divides into four (*D*, *a*, *b*, *c*, *d*), and the cell *a* projects and gives rise to the multicellular female organ. The true egg-cell (*E*, *ac*), which is called the carpogonium, is surrounded by a layer of cells. Above the carpogonium come two cells (*E*, *tp*, *t*) the upper of which is the freely projecting trichogyne or receptive organ for the spermatia. The behaviour of the nuclei has not yet been followed, but probably a fusion of male and female nuclei takes place in the carpogonium. The latter becomes divided into three cells of which the uppermost disappears, the lowest (*F*, *st*) remains sterile, while from the middle cell the asci grow out. Each ascus (*G*) produces four spindle-shaped, bicellular spores. The similarity of the sexual organs to those of the Florideae and of the lichen-forming Ascomycetes is of great interest.

Sub-Class II. Basidiomycetes (48, 49, 70, 71, 72)

The large group of the Basidiomycetes in the wide sense consists of Fungi, the mycelium of which is septate as in the Ascomycetes, but is distinguished by the loss of sexual reproduction and by the formation of basidia (p. 388), different forms of which are met with.

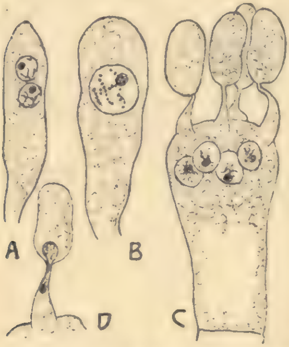


FIG. 343.—*Armillaria mellea.* *A*, Young basidium with the two primary nuclei; *B*, after fusion of the two nuclei. *Hypholoma appendiculatum*, *C*, a basidium before the four nuclei derived from the secondary nucleus of the basidium have passed into the four basidiospores; *D*, passage of a nucleus through the sterigma into the basidiospore. (After RUHLAND.)

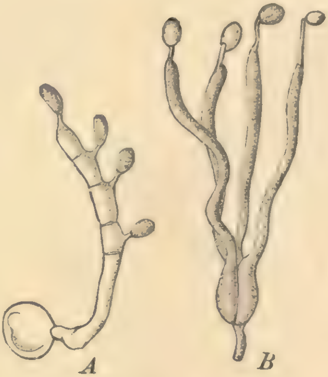


FIG. 344.—Basidia. *A*, Of a Uredineous fungus (*Endophyllum Euphorbiae silvaticae*). (after TULASNE). *B*, Of one of the Tremellineae (*Tremella lutescens*) (after BREFELD). (× 450. From v. TAVEL, *Pilze*.)

In the orders Uredineae and Auricularieae the upper portion of the basidium is divided by transverse walls into four cells; each cell bears on a thin stalk (sterigma), arising near the upper end, a single spore (Fig. 344 *A*). In the Tremellineae, on the other hand, the basidium is divided by longitudinal walls into four cells, each of which continues into a long tubular sterigma (Fig. 344 *B*). The basidium in the Hymenomycetes and Gasteromycetes is unicellular, and bears as a rule four spores at the summit; these may be sessile or situated on sterigmata (Figs. 343, 355).

The Ustilagineae are of interest since in one family the basidia are divided, and not always strictly four-celled, while in the other the basidia are undivided. The number of spores produced is not a definite one but often very large.

In addition to conidiophores differentiated as basidia, the Basidiomycetes produce other forms of conidia as accessory fructifications in many species. These appear in the Ustilagineae as the smut-spores, and as the rust-spores in the Uredineae. In these groups the basidia arise directly from spores of this kind (Figs. 344 *A*, 346). In other Basidiomycetes, if a few simple forms are disregarded, the basidia are always borne upon or within more or less complicated fructifications. The layer in which the basidia are associated together is termed the hymenium.

Order 1. **Ustilagineae** (**Smut-Fungi**) ($^{48, 49, 73}$)

The Ustilagineae are parasites, and their mycelium is found ramifying in higher plants, usually in definite organs, either in the leaves and stems, or in the fruit or stamens. The Gramineae in particular serve as host plants; certain species of Ustilagineae are in a high degree injurious to cereals, and produce in the inflorescences of Oats, Barley, Wheat, Millet, and Maize the disease known as Smut.

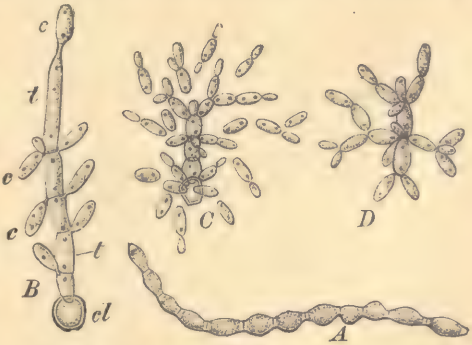


FIG. 345.—*A*, *Ustilago olivacea*. Mycelial hypha in process of forming smut-spores (× 400). *B-D*, *Ustilago segetum*: *B*, germinating smut-spore (*cl*), cultivated in nutrient solution; *t*, transversely septate basidium with lateral and terminal basidiospores (conidia) (*c*) (× 450); *C*, germinating smut-spore lying in the nutrient solution surrounded by abstricted conidia, which are multiplying by budding (× 200); *D*, an aggregation of budding conidia (× 350). (After BREFELD, from v. TAVEL, *Pilze*.)

The mycelium ultimately produces resting-spores by the formation of additional transverse walls, and by the division of its profusely branched hyphæ into short swollen cells (Fig. 345 *A*). The cells become rounded off and converted into spores, within a gelatinous envelope, which, however, eventually disappears. The spores then become invested with a new, thick, double wall. In this way the mycelium is transformed into a dark brown or black mass of spores. These Smut-spores, brand-spores, or resting-spores are scattered by the wind, and germinate only after an interval of rest, producing the basidia in the succeeding spring; the formation of these is characteristically different in the two families of the Ustilaginaceae and the Tilletiaceae.

The most important genus of the **Ustilaginaceae** is *Ustilago*. *Ust. Avenae*, *U. Hordei*, and *U. Tritici segetum*, which were formerly united as *U. Carbo*, cause the "smut" or "brand" of Oats, Barley, and Wheat. The mycelium penetrates the ovary, and forms dark brown, dust-like masses of escaping resting-spores. *U. Maydis* produces on the stalks, leaves, and inflorescences of the Maize tumour-like swellings filled with brand-spores in the form of a black powder. Other species live on the leaves of different grasses; while *U. violacea* (= *U. antherarum*) occurs in the anthers of various Caryophyllaceae (*e.g. Lychnis*, *Saponaria*), and fills the pollen-sacs with brand-spores.

The brand-spores of *Ustilago* fall to the ground, and after a period of rest give rise, on germinating, to a short tube (promycelium) which becomes septated by three or four transverse walls (Fig. 346 *B*), and, functioning as a basidium, produces ovate basidiospores or conidia (sporidia), both laterally from the upper ends of the intermediate cells, and also from the tip of the terminal cell. When abundantly supplied with nourishment, as when cultivated in a nutrient solution, conidia are continuously abstricted in large numbers (Fig. 345 *C*), and then multiply further by budding, cell-fusions or union of nuclei frequently occurring as a preliminary (*C*, *D*). After the food-supply of the substratum is exhausted, the conidia grow out into mycelial hyphæ. The formation of the conidia in the damp manured soil of the grain fields is accomplished during a saprophytic mode of existence, but the hyphal filaments which are eventually produced become parasitic, and penetrate the young seedlings as far as the apical cone where the inflorescence takes its origin. The mycelium continues its development in the inflorescence, and ultimately terminates its existence by the production of brand-spores. No conidia are formed on the host plant itself.

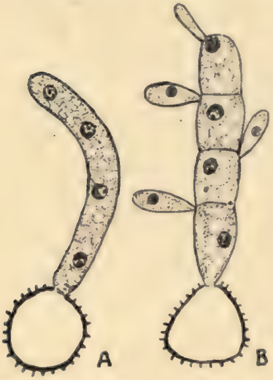


FIG. 346. — *Ustilago Scabosiae*. *A*, young basidium with four nuclei formed on germination of the resting spore; *B*, spore-formation on the 4-celled basidium. (After HARPER.)

In addition to the infection of young plants either resting-spores or the conidia resulting from their germination may be carried to the stigmas of the grass-flowers (74) and germinating there produce a mycelium which penetrates to the young seeds and passes the winter in the embryo-plants. Such infection of the flowers may alone take place as in *Ustilago Tritici*, *U. Hordei*, and *U. antherarum*, or the seedling may more often be infected as in *U. Avenae*, *U. Sorghi*, *U. Panici miliacei*, *U. Crameri*. The Smut of Maize can infect all parts of the plant while in a young state and the disease is limited to the infected spots.

The life-history of the **Tilletiaceae** is similar to that of the Ustilaginaceae. The best-known species are *Tilletia Tritici* (= *T. Caries*) and *Tilletia laevis*, the fungi of the stink-brand of wheat. The resting-spores fill the apparently healthy grains and smell like decayed fish. In the first-named species the resting-spores are reticulately thickened; those of *T. laevis*, on the other hand, are smooth-walled. Unlike the Ustilaginaceae, the germ-tube gives rise only at its apex to filiform basidiospores, which are disposed in a whorl, and consist of four to twelve spores (Fig. 347 *A*). The basidiospores also exhibit the peculiarity that they coalesce with one another in pairs in an H-form. Such cell fusions also occur between germinating conidia of the Ustilagineae, but are not accompanied by nuclear fusions. The filiform spores germinate readily, and produce sickle-shaped conidia at the apex of the germ-tubes (Fig. 347 *C*). When abundantly supplied with food material, the germ-tubes grow into large mycelia, from which such sickle-shaped conidia are so abundantly abstricted that they have the appearance of a growth of mould (*D*).

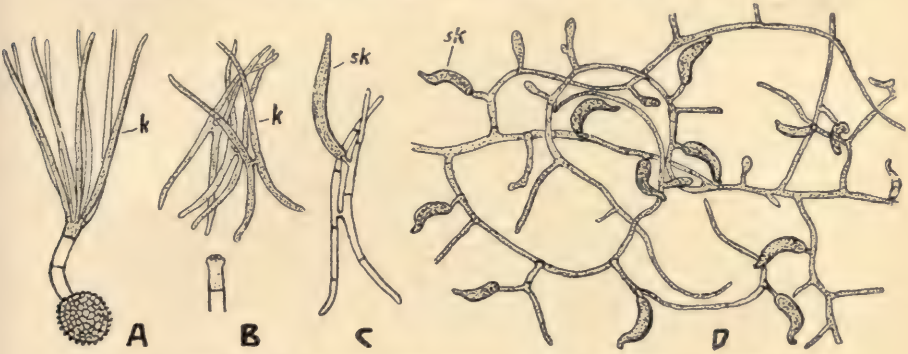


FIG. 347.—*Tilletia Tritici.* *A*, the basidium developed from the brand-spore bearing at the end four pairs of spores *k* (× 300); *B*, the dispersion of the spores which have fused in pairs (× 250); *C*, one of the paired spores germinating and bearing a sickle-shaped conidium *sk* (× 400). *D*, Mycelium with sickle-shaped conidia (× 350). (After BREFELD.)

Thus *Tilletia*, unlike *Ustilago*, produces conidia of two forms; but in other particulars the development of both groups is the same.

The young resting-spores, and the cells of the mycelium from which they are produced contain each two nuclei which fuse with one another as the spore becomes mature. The cells of the basidia, and the basidiospores are all uninucleate, only the secondary conidia of *Tilletia* being again binucleate.

Order 2. Uredineae (Rust Fungi) (75–78)

The mycelium of the Uredineae lives parasitically in the intercellular spaces of the tissues of the higher plants, especially in the leaves, and gives rise to the widely spread diseases known as Rusts. Their more varied spore-formation is a distinguishing feature as contrasted with the Ustilagineae.

As in the latter order, the basidia are not produced directly on the mycelium but on the germination of a special type of spore, teleutospores or winter spores, which are characteristic of all Uredineae. The teleutospores arise in small clusters beneath the epidermis of the diseased leaf from the ends of hyphæ; frequently two or more form a short chain. They are thick-walled resting-spores and persist through the winter (Fig. 348, 1, 5*t*). The group of spores usually bursts through the epidermis. At first the spores, like the cells of the mycelium which bears them, have two nuclei, but the nuclei fuse before the spore is ripe.

In the germination of the teleutospore a basidium (promycelium) grows from each cell (Fig. 348, 2); it becomes divided by transverse septa into a row of four cells from each of which a sterigma bearing a single uninucleated basidiospore (sporidium) is produced. The sporidia are dispersed by the wind and germinate in the spring on the leaves of host plants (which may be of the same or different species from the one on which the teleutospores were produced), giving rise to an intercellular mycelium, all the cells of which are uninucleate. From this mycelium organs of two kinds arise, spermogonia on the upper surface of the leaf and æcidia on the lower surface.

The SPERMOGONIA (Fig. 349) are flask-shaped structures, the base of which is covered with the projecting ends of hyphæ; from these are abstricted spermatia, each of which has a single nucleus. Morphologically they are completely comparable to the similarly named male sexual organs of some Ascomycetes; among the Basidiomycetes they persist only in the Uredineae, and even in them are no longer functional and may be completely wanting. In nutrient solutions the spermatia may put out short germ-tubes but are not capable of infecting the host plant.

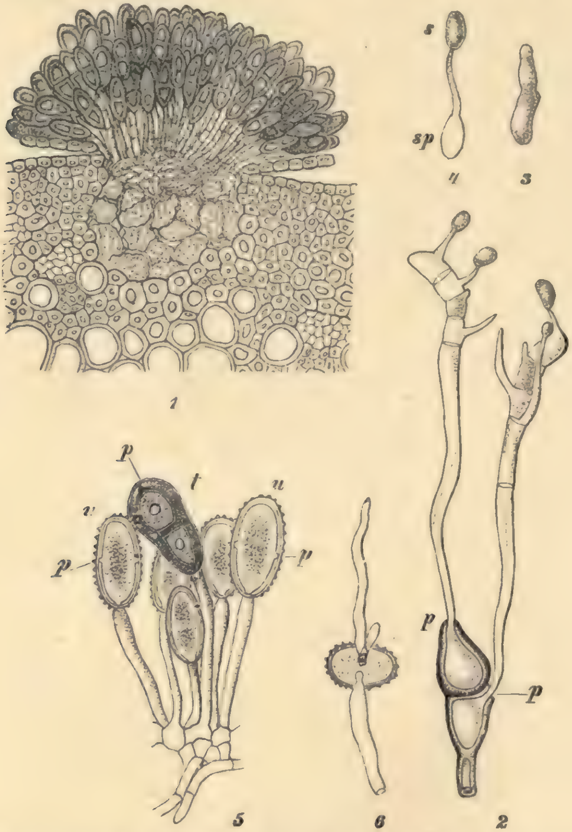


FIG. 348.—*Puccinia graminis.* *1*, Transverse section through a grass-haulm with group of teleutospores; *2*, germinating teleutospore with two basidia; *3*, vegetative. *4*, fructifying germinating basidiospore; the latter has formed a secondary spore, not having been able to infect a host plant; *5*, a portion of a group of uredospores (*u*) and teleutospores (*t*); *p*, the germ-spores; *6*, germinating uredospore. (*1*, *2*, *3*, *4*, after TULASNE; *5*, *6*, after DE BARY; 1 × 150, 2 × circa 230, 3, 4 × 370 5 × 300, 6 × 390, from v. TAVEL, *Pilze*.)

The ÆCIDIA (Fig. 350) are cup-shaped fructifications, which when young are closed, but later open; from the ends of the hyphæ numerous closely associated chains of spores are abstricted. As a rule the enveloping layer or peridium of the æcidium is formed of thick-walled cells corresponding to the sterilised peripheral rows of spores. In *Phragmidium violaceum*, which occurs on Blackberry leaves and has been fully investigated by Blackman (76), the hyphæ beneath the epidermis when about to give rise to an æcidium first cut off a sterile cell, which undergoes no further development, from their ends (Fig. 351 *A*). The cell below this increases in size; it has at first only a single nucleus but becomes binucleate by the passage of a nucleus into it from an adjoining mycelial cell. The two nuclei do not fuse. The binucleate cell undergoes successive divisions into a chain of spore-mother-cells, each of which has a pair of nuclei; and from each spore-mother-cell an upper binucleate æcidiospore and a sterile intercalary cell, which is also binucleate but soon shrivels up, are derived by a transverse division (*B*, *C*).

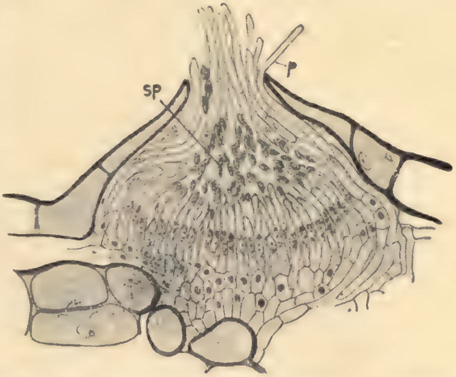


Fig. 349.—*Gymnosporangium clavariaeforme.* A spermogonium rupturing the epidermis of a leaf of *Crataegus*; *sp*, spermatia; *p*, sterile paraphyses. (After Blackman.)

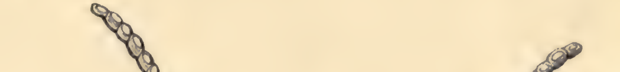


Fig. 350.—*Puccinia graminis.* Æcidium on *Berberis vulgaris*; *ep*, epidermis of lower surface of leaf; *m*, intercellular mycelium; *p*, peridium; *s*, chains of spores. (× 142.)

According to Christman (76) the development of the æcidiospores in *Phragmidium speciosum* (Fig. 352), which is parasitic on *Rosa*, proceeds somewhat differently. Here also the ends of the hyphæ (*A*) divide into a terminal sterile cell and a lower fertile cell (*B*), but the fertile cells fuse in pairs with one another, the upper portions of the separating walls breaking down (*C*). The two nuclei lie side by side and divide simultaneously (conjugate division). Two of the daughter-nuclei remain in the lower part and two pass to the upper portion of the dividing cell, and this upper portion is separated by a transverse wall as the first spore-mother-cell (*D*). In other respects the formation of the æcidiospores proceeds as described above. A peridium is not formed in *Phragmidium*.

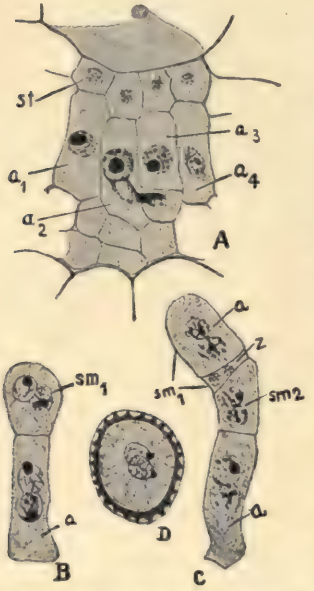


FIG. 351.—*Phragmidium violaceum*. *A*, portion of a young æcidium; *st*, sterile cell; *a*, fertile cells; at a_2 the passage of a nucleus from the adjoining cell is seen; *B*, formation of the first spore-mother-cell sm_1 from the basal cell *a* of one of the rows of spores; *C*, a further stage in which from sm_1 the first æcidiospore (*a*) and the intercalary cell (*z*) have arisen; sm_2, the second spore-mother-cell; *D*, ripe æcidiospore. (After BLACKMAN.)

The ripe, binucleate æcidiospores (Fig. 351 *D*) are shed and infect a new host plant. Each spore gives rise to an intercellular mycelium which soon proceeds in the summer to bear uredospores or summer spores. These appear in small circular or linear groups and arise singly from the enlarging terminal cells of the hyphæ (Fig. 348, 5, 6). They have two nuclei like all the cells of the mycelium developed from the æcidiospore. They serve commonly to ensure the spread of the fungus in the summer. Later, either in the same or in distinct sori the teleutospores are formed, and in these the fusion of the two nuclei to a single one takes place; such a fusion as a rule is found to take place in the young basidium.

The two types of cell-fusion in the formation of the æcidium are also found in other Uredineae, and must be regarded as replacing a formerly existing method of fertilisation. If we attempt to derive the Uredineae from the Ascomycetes the spermatia must be regarded as now functionless male cells, and the so-called fertile cells in the young æcidium as corresponding to carpogonia. Extending the comparison further the mycelium proceeding from the æcidiospore in the Uredineae and the uredospores and teleutospores borne on it, together with the basidia, formed by the latter, would together correspond to the asexual generation (sporophyte) of the Ascomycetes. The basidiospores would thus correspond to the ascospores, while the mycelium proceeding from the basidiospore would be equivalent to the sexual generation (gametophyte).

The life-history of the Rust-fungi is thus a complicated one. The several forms of spore may appear in the course of the year on the one host, such Uredineae being termed autœcious. On the other hand the spermogonia and æcidia may occur on one species of host plant, and the uredospores and teleutospores on another, often unrelated, plant. In these heterœcious species there is thus an alternation of host plants (^{77}).

An example of an heterœcious Rust-Fungus is afforded by *Puccinia graminis*, the rust of wheat. It develops its uredospores and teleutospores on all the green parts of Gramineae, especially of Rye, Wheat, Barley and Oats. The æcidia and spermogonia of this species are found on the leaves of the Barberry (*Berberis* *vulgaris*). In the spring the hibernating double teleutospores give rise to transversely septate basidia, from which the four basidiospores are abstricted (Fig. 348, 2). These are scattered by the wind, and if they fall on the leaves of the Barberry they germinate at once. The germ-tube penetrates the cuticle, and there forms a mycelium which gives rise to spermogonia on the upper side of the leaf, and to æcidia on the under side (Fig. 350). This form of the fungus is known as *Aecidium Berberidis.* On the rupture of the peridium the reddish-yellow æcidiospores are conveyed by the wind to the haulms and leaves of grasses, upon which alone they can germinate. The mycelium thus developed produces at first uredospores (Fig. 348, 5). They are unicellular, studded with warty protuberances, and provided with four equatorially disposed germ-pores. In consequence of the reddish-yellow fat globules contained in the protoplasm of the spores, the fructification forms red markings (formerly termed *Uredo linearis*) on the epidermis of the host plant. The uredospores are capable of germinating at once on the wheat, and thus the rust disease is quickly spread. Towards the end of the summer the same mycelium produces the dark brown, thick-walled teleutospores, which in this species are always double, being united in pairs. Each teleutospore is provided with one germ-pore, and on germination in the succeeding year the cycle is begun afresh. The mycelium of the Uredo form may hibernate in winter wheat, and thus the rust may appear in the spring without the previous formation of basidiospores or of æcidia.

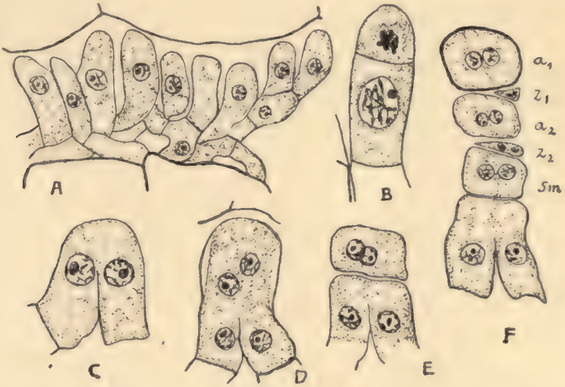


FIG. 352.—*Phragmidium speciosum.* *A*, The first rudiment of an æcidium beneath the epidermis of a leaf of *Rosa*; *B*, the division of the end-cell of a hypha into the upper, transitory, sterile cell and the lower fertile cell; *C*, conjugation of two adjoining fertile cells; *D*, later stage in which the first nuclear division is completed; *E*, abstriction of the first æcidiospore mother-cell; *F*, chain of æcidiospores (a_1, a_2) separated by intercalary cells (z_1, z_2); *sm*, the last-formed spore-mother-cell still undivided. (After CHRISTMAN.)

Other common Rusts on grasses or cereals which are closely related to *Puccinia graminis* are *Puccinia dispersa* on the Rye, which develops its æcidia on *Anchusa*, and *P. triticina* and *P. glumarum*, which occur respectively on Wheat and on Wheat, Rye and Barley. The æcidia of these latter forms are unknown.

All Uredineae do not exhibit so complicated a course of development as *Puccinia graminis.* Certain species produce only basidia from germinating teleutospores, or, in addition to teleutospores, only uredospores which are developed on the same host. Others produce spermogonia and æcidia, and afterwards teleutospores, but no uredospores. In the case of the heterœcious species, it is only possible to demonstrate the connection between the different spore-forms by means of culture experiments. So long as the relation of the different forms was not known, it was customary to designate each by a special generic name; the Uredo forms as *Uredo*; the Æcidia, according to their structure, as *Aecidium*, *Roestelia*, *Peridermium*, etc. The generic name is now determined by the characters of the teleutospores, since they exhibit the most characteristic distinctions.

In those Uredineae which no longer possess æcidia and spermogonia, the cells of the vegetative mycelium arising from the basidiospore are uninucleate, but subsequently, before the formation of the teleutospores, binucleate cells are found. Further research is needed to show how the binucleate condition is arrived at; at all events, these forms exhibit a still further reduction of the sexual process and of the alternation of generations.

Order 3. Auricularieae

The basidia, as in the case of the Uredineae, are transversely septate, with four spores. Only a few forms are included in this order. Among the most familiar is *Auricularia sambucina* (Judas' ear), found on old Elder stems. It has gelatinous, dark brown fructifications, which are shell-shaped and bear on their inner sides the basidial hymenium.

Order 4. Tremellineae

The basidia are longitudinally divided (Fig. 344 *B*). The hymenium is situated on the upper surface of the fructifications, which are generally gelatinous and irregularly lobed or folded. The few genera included in this order are saprophytic on decaying wood and tree-trunks, on the surface of which the fructifications are produced.

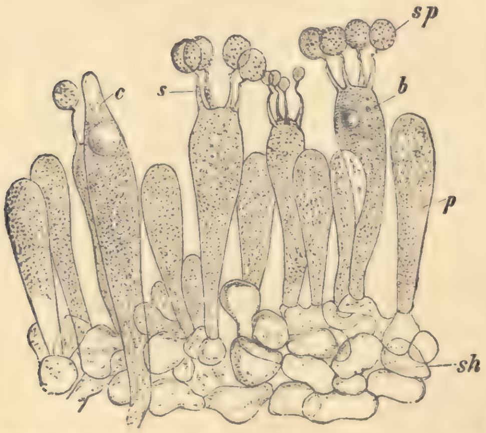


FIG. 353.—*Russula rubra*. Portion of the hymenium. *sh*, Subhymenial layer; *b*, basidia; *s*, sterigmata; *sp*, spores; *p*, paraphyses; *c*, a cystid. (× 540.)

Order 5. Hymenomycetes (63, 72)

The basidia are undivided, and bear four spores at the apices of slender sterigmata (Fig. 353 *sp*). In the simplest forms these basidia spring directly from the mycelium, but in the great majority of cases fructifications are produced, which bear definite hymenial layers, composed, in addition to the basidia, of paraphyses (Fig. 353 *p*), and also of sterile cystids (*c*) or club-shaped tubes characterised by their larger diameter and more strongly thickened wall.

Most of the Hymenomycetes develop their profusely branched, white mycelium in the humus soil of forests, in decaying wood or on dying tree trunks, and produce fructifications, commonly known as toad-stools, protruding from the substratum. The mycelium of the forms vegetating in the soil spreads farther and farther, and dying in the centre as it exhausts the food material of the substratum, occupies continually widening concentric zones. In consequence of this mode of growth, where the development has been undisturbed, the fructifications, which appear in autumn, form the so-called fairy rings. A few Hymenomycetes are parasitic, and vegetate in the bark or wood of trees. Of such parasitic forms *Armillaria mellea*, whose mycelium vegetates between the bark and wood of Conifers and other trees, is a familiar example. The profusely branching mycelial hyphæ (Fig. 354) become interwoven into flat, black strands from which fine, hair-like hyphæ are sent out and penetrate the wood for the absorption of nourishment. It is from these sub-cortical strands, known as RHIZOMORPHA, that the stalked, capitate fructifications are eventually produced. In addition to the subcortical strands, subterranean rhizomorphs are developed which pervade the soil and infect the roots of other trees. The rhizomorphs may be regarded as a form of sclerotia. This fungus is one of those that give rise to photogenic substances which cause the phosphorescence of the infected wood (79).

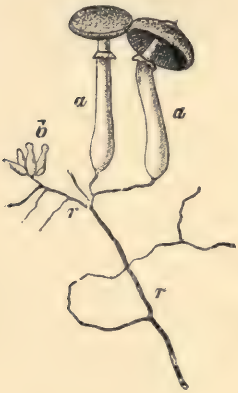


FIG. 354.—*Armillaria mellea.* Portion of a rhizomorph strand (*r*) with mature (*a*) and young (*b*) fructifications. (After HARTIG, from v. TAVEL ; ½ nat. size.)

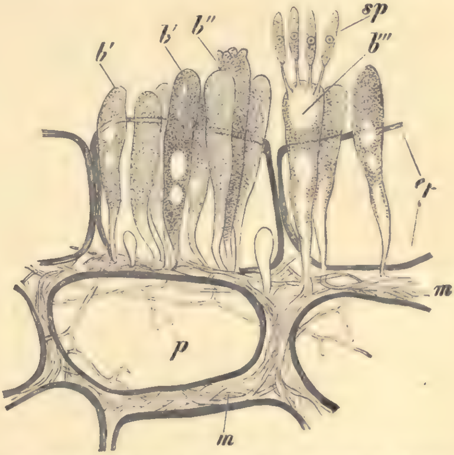


FIG. 355. — *Exobasidium Vaccinii.* Transverse section through the periphery of a stem of *Vaccinium* ; *ep*, epidermis ; *p*, cortical parenchyma ; *m*, mycelial hyphæ ; *b'*, protruding basidia without sterigmata ; *b''*, with rudimentary sterigmata ; *b'''*, with four spores. (After WORONIN, × 620.)

The Hymenomycetes are further classified according to the increasing complexity exhibited in the structure of their basidial fructifications.

1. In a few genera no distinctive fructifications are formed, and the basidia spring in irregular groups directly from the mycelium. *Exobasidium Vaccinii* may be taken as a type of this form. The mycelium of this fungus, which is widely spread in Europe, is parasitic in the Ericaceae, especially on species of *Vaccinium* ; it causes hypertrophy of the infected parts. The basidia are formed in groups under the epidermis, which they finally rupture (Fig. 355). In this genus, as in

many others, accessory fructifications are developed, and spindle-shaped conidia are abstricted from the mycelium on the surface of the host plant, before the formation of the basidia.

2. In the group of the **Thelephoreae**, distinctive fructifications of a simple type are found. They form on the trunks of trees either flat, leathery incrustations bearing the hymenium on their smooth upper surfaces; or the flat fructifications become raised above the substratum and form bracket-like projections, which frequently show an imbricated arrangement, and bear the hymenium on the under side (*e.g. Stereum hirsutum*, common on the stems of deciduous trees).

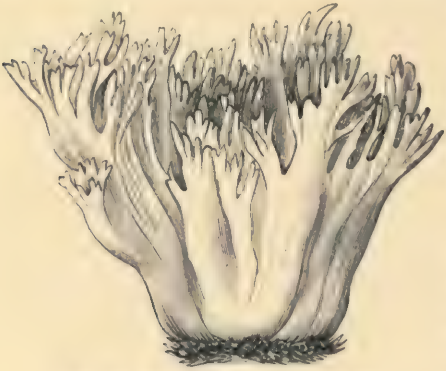


FIG. 356.—*Clavaria botrytis.* (Nat. size.)

3. The fructifications of the **Clavarieae** form erect whitish or yellow-coloured bodies, either fleshy and club-shaped or more or less branched, in a coral-like fashion. The larger, profusely branched forms of this group are highly esteemed for their edible qualities; in particular, *Clavaria flava*, whose fleshy, yellow-coloured fructifications are often ten centimetres high, also *Clavaria botrytis* (Fig. 356), which has a pale red colour. *Sparassis crispa*, which grows in sandy soil in Pine woods, has fructifications half a metre in diameter, with compressed, leaf-like branches.

4. The **Hydneae** have fructifications with spinous projections over which the hymenium extends. In the simpler forms the fructifications have the appearance of incrustations, with spinous outgrowths projecting from the upper surface; in other cases they have a stalk, bearing an umbrella-like expansion, from the under side of which the outgrowths depend. The latter form is exhibited by the edible fungi *Hydnum imbricatum*, which has a brown pileus 15 cm. wide, with dark scales on the upper surface, and *Hydnum repandum* (Fig. 357), with a yellowish pileus.

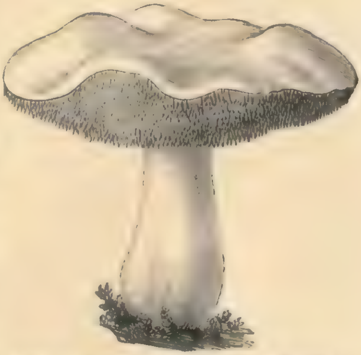


FIG. 357.—*Hydnum repandum.* (Reduced.)

5. In the **Polyporeae**, a group containing numerous species, the stalked or sessile and bracket-shaped fructifications are indented on the under side with pit-like depressions, or deep winding passages, or covered with a layer of tubes, closely fitted together and lined by the hymenium. To this family belongs the genus *Boletus*, occurring on the soil of woods, which has a large, thick-stalked pileus, covered on the under side with a layer of narrow dependent tubes. Although many species of this genus are edible (*e.g. B. edulis*), others are exceedingly poisonous, in particular *B. Satanas* (Fig. 360). The stalk of the latter fungus is a yellow to reddish-purple, or has red reticulate markings, while the

pileus, which may be 20 cm. wide, is yellowish-brown on its upper surface, but on the under side is at first blood-red, becoming later orange-red. Of the numerous species of the genus *Polyporus*, *P. fomentarius*, Touch-wood, is used in medicine.

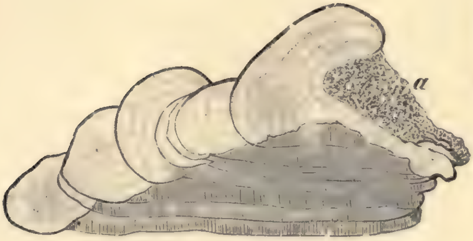


FIG. 358.—*Polyporus igniarius.* Section through an old fructification, showing annual zones of growth; *a*, point of attachment. (½ nat. size.)

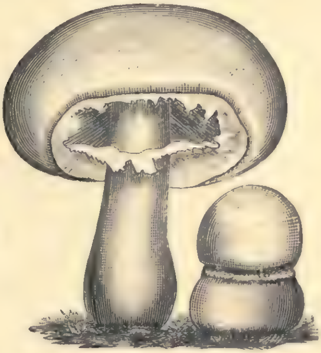


FIG. 359.—*Psalliota campestris* (= *Agaricus campestris*). To the right, a young fructification. (Reduced.)

Its mycelium is parasitic in deciduous trees, especially the Beech, and produces large, bracket or hoof-shaped, perennial fructifications, 30 cm. wide and 15 cm. thick. They have a hard, grey external surface, but inside are composed of softer, more loosely woven hyphæ, and were formerly used for tinder. The narrow tubes of the hymenium are disposed on the under side of the fructifications in successive annual layers. *P. igniarius* (Fig. 358), which is often found on Willows, and has a similar structure, has a rusty-brown colour, and furnishes, since it is much harder, a poorer quality of tinder. *Polyporus officinalis* with an irregularly tuberous

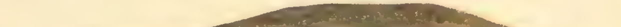


FIG. 360.—*Boletus Satanas.* (After KROMBHOLZ, ½ nat. size.) *POISONOUS.*

white fructification occurs on Larches in South Europe; it contains a bitter resinous substance and is also used in medicine.

Many parasitic Polyporeae are highly injurious to the trees attacked by them; thus *Heterobasidion annosum* often causes the death of whole forests of Pines and Spruce Firs. *Merulius lacrymans* (80) is an exceedingly dangerous saprophytic species, attacking and destroying the timber of damp houses. The mycelium of this fungus forms large, white, felted masses with firmer branched strands which serve to conduct water and food substances. It gives rise to outspread, irregularly shaped, pitted fructifications of an ochre or rusty-brown colour, and covered with a hymenial layer. Good ventilation of the infected space is the best remedial measure.

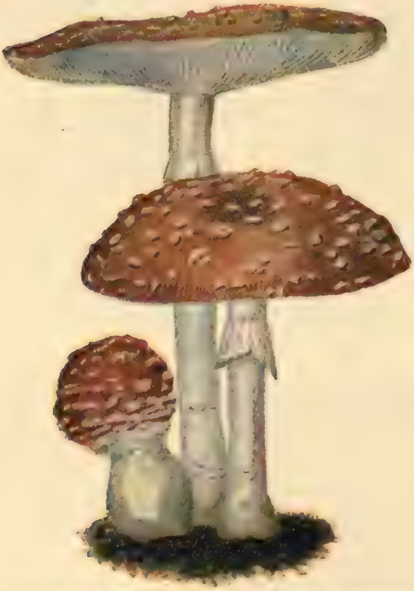


FIG. 361.—*Amanita muscaria.* (½ nat. size.) *POISONOUS.*

6. The **Agaricineae**, which include the greatest number of species, have stalked fructifications, commonly known as Mushrooms and Toadstools. The under side of the pileus bears a number of radially disposed lamellæ or gills which are covered with the basidia-producing hymenium. In the early stages of their formation the fructifications consist of nearly spherical masses of interwoven hyphæ, in which the stalk and pileus soon become differentiated. The rudiments of the stalk and pileus are at first enclosed in a loosely woven envelope, the VOLVA. In the course of the further development and elongation of the stalk the volva is ruptured, and its torn remnants form a ring or sheath at the base of the stalk, and in many cases (as in the "Fly Mushroom," *Amanita muscaria*), are still traceable in the white scales conspicuous on the red surface of the pileus (Fig. 361). In addition to the volva many Agaricineae develop a so-called VELUM, consisting of a thin membrane of hyphal tissue which extends in young fructifications from the stalk to the margin of the pileus, but is afterwards ruptured, and remains as a ring of tissue encircling the stalk (Fig. 359).

Many of the Mushrooms found growing in the woods and fields are highly esteemed as articles of food. Of edible species the following may be named: the common Field-Mushroom, now extensively cultivated, *Psalliota campestris* (Fig. 359), with whitish pileus and lamellæ at first white, then turning flesh-colour, and finally becoming chocolate-coloured; *Cantharellus cibarius*, having an orange-coloured pileus; *Lactarius deliciosus*, which has a reddish-yellow pileus, and contains a similarly coloured milky juice in special hyphal tubes; *Lepiota procera*, whose white pileus is flecked with brown scales; *Amanita caesarea* with an orange pileus bearing a few white scales and yellow lamellæ.

Of the poisonous Agaricineae the following are best known: *Amanita muscaria* (Fig. 361); *Amanita bulbosa* (Fig. 362) with whitish or yellowish pileus and the stalk swollen at the base; *Russula emetica*, with a red pileus and white lamellæ; *Lactarius torminosus*, having a shaggy, yellow or reddish-brown pileus and white milky juice.

Rozites gongylophora, found in South Brazil, is of especial biological interest. According to A. MÖLLER, this species is regularly cultivated in the nests of the leaf-cutting ants. Its mycelium produces spherical swellings at the ends of the hyphæ, which become filled with protoplasm, the so-called Kohl-rabi heads, and serve the ants as food material. The ants prevent the development of the accessory conidial fructifications peculiar to this fungus, and thus continually maintain the mycelium in their nests in its vegetative condition. The fructifications, which rarely occur on the nests, resemble those of *Amanita muscaria*, with which *Rozites* is nearly allied. According to HOLTERMAN, the mycelium of *Agaricus rajap* is cultivated in their nests by termites in tropical Asia ([81]).

ECONOMIC USES.—*Polyporus fomentarius* (FUNGUS CHIRURGORUM). *Polyporus officinalis* (=*Boletus laricis*) gives AGARICUS ALBUS, AGARICINUM, and ACIDUM AGARICINUM.

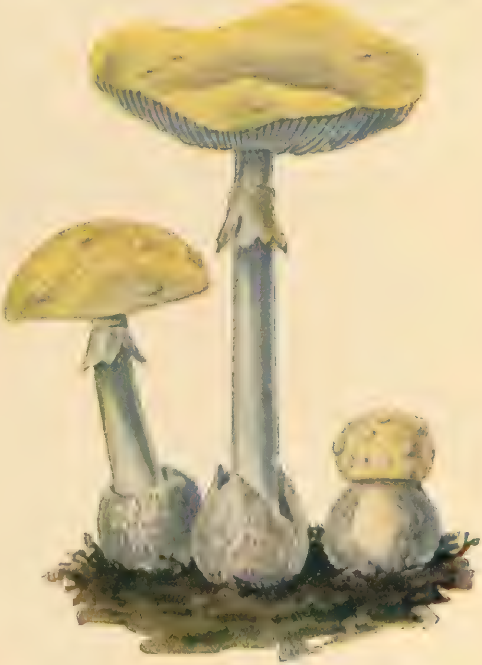


FIG. 362.—*Amanita bulbosa*. (½ nat. size.) *POISONOUS.*

Order 6. Gasteromycetes ([63])

The Gasteromycetes are distinguished from the Hymenomycetes by their closed fructifications, which open only after the spores are ripe, by the rupture of the outer hyphal cortex or PERIDIUM. The spores are formed within the fructifications in an inner mass of tissue termed the GLEBA; it contains numerous chambers, which are either filled with loosely interwoven hyphæ with lateral branches terminating in basidia, or their walls are lined with a basidial hymenium.

The Gasteromycetes are saprophytes, and develop their mycelium in the humus soil of woods and meadows. Their fructifications, like those of the Hymenomycetes, are raised above the surface of the substratum, except in the group of the Hymenogastreae, which possesses subterranean, tuberous fructifications resembling those of the Tuberaceae.

The fructifications of *Sclerodema vulgare* (Fig. 363, 1) have a comparatively simple structure. They are nearly spherical, usually about 5 cm. thick, and have a thick, light brown, leathery peridium which finally becomes cracked and ruptured at the apex. The gleba is black when ripe, and contains numerous chambers filled with interwoven hyphæ which produce lateral, pear-shaped basidia with four sessile spores (Fig. 363, 2). This species, which is considered poisonous, is sometimes mistaken for one of the Truffle Fungi.

The genera *Bovista* and *Lycoperdon* (Fig. 363 3) (Puff-balls) have also spherical fructifications, which are at first white, and later of a brown colour. In the last-named genus they are also stalked, and in the case of *Lycoperdon Bovista* may even become half a metre in diameter. The peridium is formed of two layers; the outer separates at maturity, while the inner dehisces at the summit. The hymenial layer of basidia, in the fungi of this group, lines the chambers of the gleba. The chambers are also provided with a fibrous capillitium consisting of brown, thick-walled, branched hyphæ which spring from the walls, and aid in distributing the spores. The fructifications are edible while still young and white. When mature they contain urea which is not elsewhere found in plants.

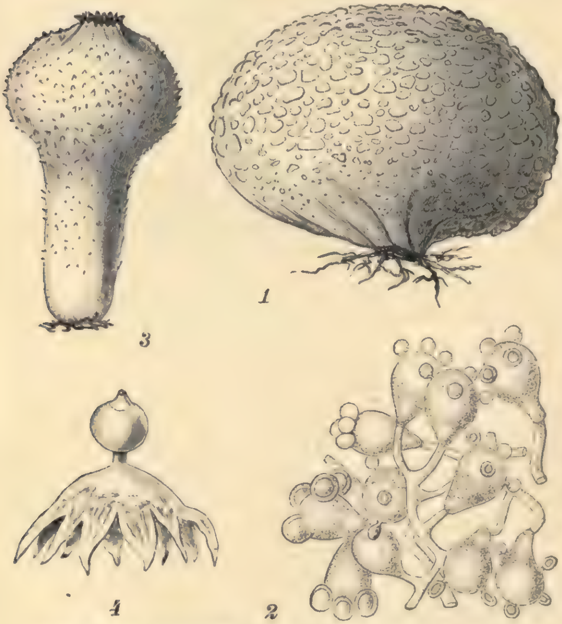


Fig. 363.—*1*, *Scleroderma vulgare*, fructification; *2*, basidia of same. (After Tulasne.) *3*, *Lycoperdon gemmatum*; *4*, *Geaster granulosus*. (*1*, *3*, *4* nat. size; *2* enlarged.)

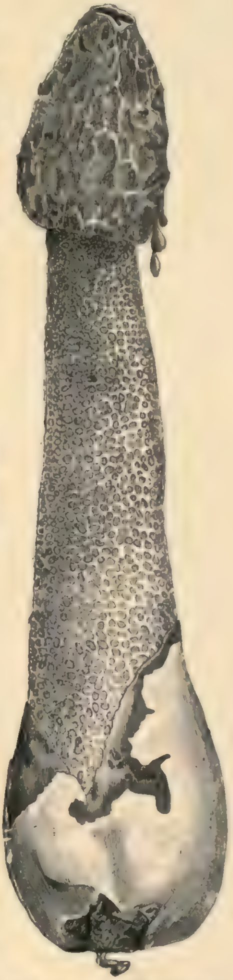


Fig. 364.—*Phallus impudicus*. (After Krombholz, ½ nat. size.)

In the related genus *Geaster* (Earth-star) (Fig. 363, 4) the peridia of the nearly spherical fructifications are also composed of two envelopes. When the dry fruit dehisces, the outer envelope splits into several stellate segments and the inner layer of the peridium becomes perforated by an apical opening.

The highest development of the fructifications is exhibited by the **Phalloideae** ([82]), of which *Phallus impudicus* (Stink-horn) is a well-known example. This fungus is usually regarded as poisonous. It was formerly employed in a salve as a remedy for gout. Its fructification recalls that of the discomycetous *Morchella*, but it has quite a different manner of development. A fructification of this species of *Phallus* is about 15 cm. high. It has a thick, hollow stalk of a white colour and is perforated with pores or chambers. Surmounting the stalk is a bell-shaped pileus covered with a brownish-green gleba which, when ripe, is converted into a slimy mass (Fig. 364). When young the fructification forms a white, egg-shaped body, and is wholly enveloped by a double-walled peridium with an intermediate gelatinous layer. Within the PERIDIUM (also termed volva) the hyphal tissue becomes differentiated into the axial stalk and the bell-shaped pileus, carrying the gleba in the form of a mass of hyphal tissue, which contains the chambers and basidial hymenium. At maturity the stalk becomes enormously elongated, and pushing through the ruptured peridium raises the pileus with the adhering gleba high above it. The gleba then deliquesces into a dropping, slimy mass, which emits a carrion-like stench serving to attract carrion-flies, by whose agency the spores embedded in it are disseminated.

CLASS XV

Lichenes (Lichens) ([48, 83-91])

The Lichens are symbiotic organisms; they consist of higher Fungi, chiefly the Ascomycetes, more rarely Basidiomycetes, and unicellular or filamentous Algae (Cyanophyceae or Chlorophyceae), living in intimate connection, and together forming a compound thallus or CONSORTIUM. Strictly speaking, both Fungi and Algae should be classified in their respective orders; but the Lichens exhibit among themselves such an agreement in their structure and mode of life, and have been so evolved as consortia that it is more convenient to treat them as a separate class.

In the formation of the thallus the algal cells become enveloped by the mycelium of the fungus in a felted tissue of hyphæ (Figs. 365, 366). The fungus derives its nourishment saprophytically from the organic matter produced by the assimilating alga; it can also send haustoria into the algal cells, and so exhaust their contents ([84]). The alga, on the contrary, derives a definite advantage from its consortism with the fungus, receiving from it inorganic substances and water, and possibly organic substances also (cf. p. 234). From the symbiosis entered into by a Lichen Fungus with an Alga, a dual organism results with a distinctive thallus, of which the form (influenced by the mode of nutrition of the independently assimilating Alga) differs greatly from that of other non-symbiotic Eumycetes, and rather resembles that of the Algae and Liverworts.

The thalli of the Lichens exhibit a great variety of forms.

The simplest Lichens are the FILAMENTOUS, with a filiform branched thallus consisting of algal filaments interwoven with fungal hyphæ. An example of such a filamentous form is presented by *Ephebe pubescens*, which is found growing on damp rocks, forming a blackish layer.

Another group is formed by the GELATINOUS Lichens, whose thallus, usually foliaceous, is of a gelatinous nature. The algae inhabiting the thalli of the gelatinous Lichens belong to the families of the Chroococcaceae and Nostocaceae, whose cell walls are swollen, forming a gelatinous mass traversed by the hyphæ of the fungus. The genus *Collema* is a European example of this group.

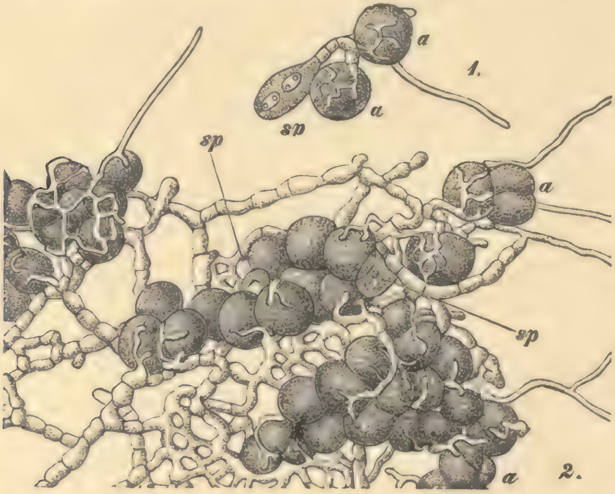


FIG. 365.—*Xanthoria parietina*. *1*, Germinating ascospore (*sp*) with branching germ-tube applied to the *Chlorococcum* cells (*a*); *2*, thallus in process of formation: *sp*, two ascospores; *p*, *Chlorococcum* cells. By the fusion of the hyphæ in the middle of the mycelium, a pseudo-parenchymatous, cortical layer has begun to form. (After BONNIER, from v. TAVEL, × 500.)

In both the filamentous and gelatinous Lichens the algae and the fungal hyphæ are uniformly distributed through the thallus, which is then said to be unstratified or HOMOIOMEROUS.

The other Lichens have stratified or HETEROMEROUS thalli. The enclosed algae are usually termed GONIDIA. They are arranged in a definite GONIDIAL LAYER, covered, externally, by a CORTICAL LAYER, devoid of algal cells and consisting of a pseudo-parenchyma of closely woven hyphæ (Fig. 366). It is customary to distinguish the three following forms of heteromerous Lichens. CRUSTACEOUS LICHENS, in which the thallus has the form of an incrustation adhering closely to a substratum of rocks or to the soil, which the hyphæ to a certain extent penetrate. FOLIACEOUS LICHENS (Fig. 367), whose flattened, leaf-like, lobed or deeply-cleft thallus is attached more loosely to the substratum by means of rhizoid-like hyphæ (rhizines), springing either from the middle only or irregularly from the whole under surface. FRUTICOSE LICHENS (Fig. 368) have a filamentous or ribbon-like thallus branched in a shrub-like manner and attached at the base. They are either erect or pendulous, or may sometimes lie free on the surface of the substratum.

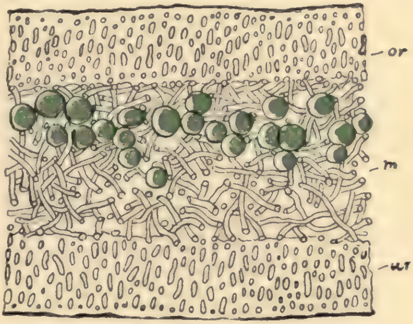


FIG. 366. — *Cetraria islandica.* Transverse section through the thallus; *or*, cortical layer of upper surface; *ur*, of the lower surface; *m*, medullary layer containing the green cells of the Alga, *Chlorococcum humicola.* (× 272.)

In nature the germinating spores of the Lichen Fungi appear to be capable of continuing their further development only when they are enabled to enter into symbiosis with the proper gonidia. For a few genera of Lichens, however, it has been determined that the fungi sometimes exist in nature without the presence of the algae; it has been shown that the tropical Lichen, *Cora pavonia* (Fig. 374), whose fungus belongs to the order Hymenomycetes, may produce fructifications even when deprived of its alga; these have a form resembling those of the fungal genus *Thelephora.* Small thalli have also been successfully grown from the spores of certain Lichen-forming Ascomycetes, cultivated without algae and supplied with a proper nutrient solution.

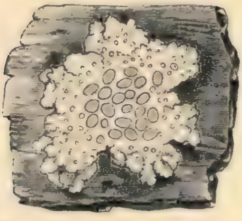


FIG. 367.— *Xanthoria parietina* on a piece of bark. (Nat. size.)

Many Lichens are able to multiply in a purely vegetative manner, by means of loosened pieces of the thallus, which continue their growth and attach themselves to the substratum with new rhizines. The majority of the heteromerous Lichens possess in the formation of SOREDIA another means of vegetative multiplication. In this process, small groups of dividing gonidia become closely entwined with mycelial hyphæ, and form small isolated bodies which, on the rupture of the thallus, are scattered in great numbers by the wind and give rise to new Lichens.

The fructifications of the Lichens are produced by the fungi, not by the algae, which are purely vegetative.

Most Lichens secrete special substances, especially in their cortical layers, among which numerous acids must be mentioned (85); according to STAHL these are useful as a protection against attack by snails (86).

1. Ascolichenes

Only a few genera of Lichens have flask-shaped perithecia, the fungus belonging to the Pyrenomycetes (*Endocarpon*, *Verrucaria*). Most genera produce, as the ascus-fruit of their fungus, cupular or discoid apothecia, sessile or somewhat sunk in the thallus. In structure they resemble those of the Pezizeae, and bear on their upper side an hymenium of asci and paraphyses. One of the commonest species of fruticose Lichens belonging to this group is *Usnea barbata*, the Beard Lichen, frequently occurring on trees and having large, fringed apothecia (Fig. 368). *Rocella tinctoria*, found widely distributed on the rocks of the African coast and East Indies, has an erect, vermiform, forked thallus from which litmus and orchil (orseille) are obtained. *Cetraria islandica*, Iceland Moss (Fig. 369), occupies an intermediate position between the fruticose and foliaceous Lichens. It has a divided, foliaceous but partially erect thallus, which is of a light bluish-green or brown colour, whitish on the under side, and bears the apothecia obliquely on its margin. This Lichen is found in mountainous regions in the northern part of the Northern Hemisphere, and also at Cape Horn; it has an official value as a demulcent. *Xanthoria parietina* (Fig. 367) may be taken as an example of one of the commonest of the foliaceous Lichens. The thallus is orange-yellow in colour, and bears numerous apothecia on its central portions. *Graphis scripta* is a well-known example of the crustaceous Lichens; its greyish-white thallus occurs on the bark of trees, particularly of the Beech, on whose surface the apothecia are disposed as narrow, black furrows resembling writing. To the crustaceous Lichens belongs also *Sphaerothallia esculenta*, growing on rocks in the steppes and deserts of North Africa and Asia. The thallus falls into small pieces the size of a pea

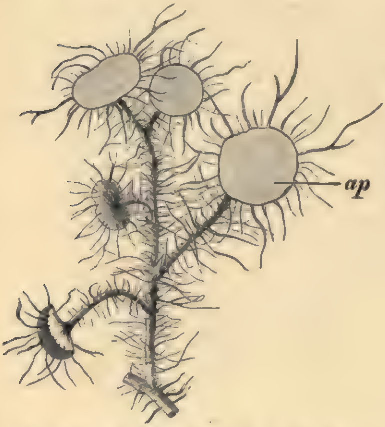


FIG. 368.—*Usnea barbata*. *ap*, Apothecium. (Nat. size.)

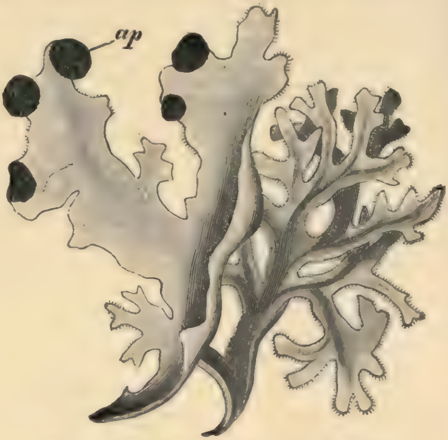


FIG. 369.—*Cetraria islandica*. *ap*, Apothecium. (Nat. size.) OFFICIAL.

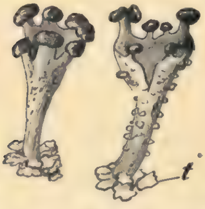


FIG. 370.—*Cladonia coccifera*. *t*, Scales of primary thallus. (Nat. size.)

which are scattered by the wind; they are utilised by the Tartars in the preparation of earth-bread.

A peculiar mode of development is exhibited by the genus *Cladonia* (87), whose primary thallus consists of small horizontal scales attached directly to the ground, from which rises an erect portion, the PODETIUM, of varying form and structure in the different species. In some cases the podetia are stalked and funnel-shaped, bearing on the margin or on outgrowths from it knob-like apothecia, which in *C. pxyidata* are brown, in *C. coccifera* (Fig. 370) bright red. In other species the erect podetia are slender and cylindrical, simple or forked; in *C. rangiferina*, Reindeer Moss, which has a world-wide distribution, particularly in the tundras of the North, the podetia are finely branched (Fig. 371), and bear the small brown apothecia at the ends of the branches. The primary thallus of this species soon disappears.

The ascus-fructifications (apothecia or perithecia) of the Lichens originate, as STAHL, and more recently BAUR (88) have shown, from carpogonia or female sexual organs, which are frequently present in large numbers on young lobes of the thallus. The carpogonium (Fig. 372) is here a multicellular filament, the lower part of which is spirally coiled, while it continues above into a trichogyne composed of elongated cells, and projecting from the surface of the thallus. All the cells are uninucleate and communicate with one another by means of pits. Those of the lower part of the filament contain abundant protoplasm. Apart from their multicellular nature these structures recall the carpogonia found in the Florideae. The spermatia, which originate in spermogonia (Fig. 373), are presumably the male sexual cells. The spermatia develop in different ways (90). In some cases the inner wall of the spermogonium is lined with simple or branched hyphal branches from the ends of which the spermatia are abstricted (*Peltigera*,

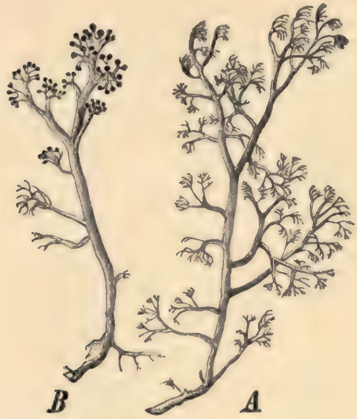


FIG. 371.—*Cladonia rangiferina*. *A*, Sterile; *B*, with ascus-fruit at the ends of the branches. (Nat size.)

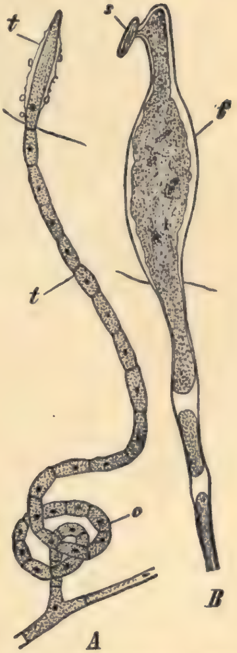


FIG. 372.—*Collema crispum*. *A*, Carpogonium (*c*) with its trichogyne (*t*) (× 405). *B*, Apex of the trichogyne with the spermatium (*s*) attached (× 1125). (After E. BAUR.)

Parmelia). In other cases the spermogonium is at first filled with a hyphal tissue in which cavities are formed later and the spermatia arise on very small and thin stalks from the cells lining the cavities. The spermatia, embedded in a slimy mass, are shed from the spermogonium and conjugate with the adhesive tip of the trichogyne (Fig. 372 *B*). After conjugation the spermatia appear empty and their nucleus has disappeared. When this has taken place the cells of the trichogyne collapse, while the cells of the coiled carpogonium swell, undergo divisions, and form the ascogonium. From the latter the ascogenous hyphæ which bear the asci are produced. The vegetative hyphæ composing the fructification and the paraphyses originate from hyphæ which arise below the carpogonium. The fructification may arise from one or from several carpogonia. The behaviour of the sexual nuclei requires further investigation. Such carpogonia have been shown to give rise to the fructifications in a large number of genera. In other genera (*Peltigera*, *Solerina*), they are reduced and the trichogyne is wanting, and the reproduction is apogamous. Spermogonia are, as a rule, not found in these cases, or are, as in the case of *Nephromium*, degenerating structures. It has been shown by A. MÖLLER (89), that the spermatia of Lichens can germinate and produce a mycelium; but this is not inconsistent with their primitively sexual nature.

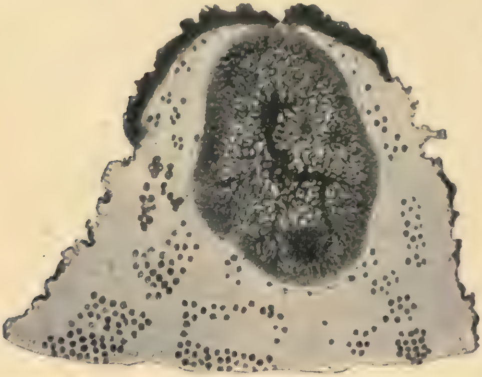


FIG. 373.—*Anaptychia ciliaris.* Ripe spermogonium. The dark round bodies within the thallus are the green Algal cells. (× 192. After GLÜCK.)

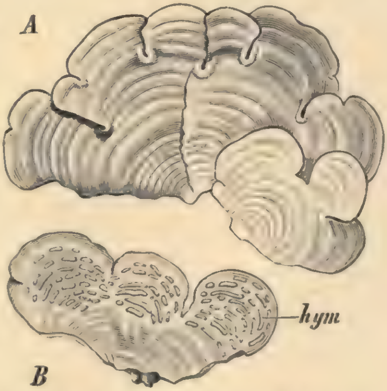


FIG. 374.—*Cora pavonia.* *A*, Viewed from above *B*, from below; *hym*, hymenium. (Nat. size.)

2. Basidiolichenes (Hymenolichenes) (91)

The Hymenolichènes are represented by the tropical *Cora pavonia*, of which the genera *Dictyonema* and *Laudatea* are only specially differentiated forms. The fungus of this Lichen belongs to the family Thelephoreae (p. 410); its flat, lobed, and often imbricated fructifications are also found entirely devoid of Algæ. In symbiosis with the unicellular Alga *Chroococcus*, it forms the fructifications of *Cora pavonia* (Fig. 374), resembling those of the Thelephoras with a channelled, basidial hymenium on the under side. Associated symbiotically, on the other hand, with filaments of the blue-green Alga *Scytonema*, if the Fungus preponderates, it produces the bracket-like Lichens of the *Dictyonema* form, found projecting from the limbs of trees with a semicircular or nearly circular thallus, having the hymenium on the under side. When the shape of the thallus is determined by the Alga, a Lichen of the *Laudatea* form occurs as felted patches of fine filaments on the bark of trees, with the hymenium on the parts of the thallus which are turned away from the light.

OFFICIAL.—The only representative of the Lichens is *Cetraria islandica* (LICHEN ISLANDICUS). *Sticta pulmonacea* is also used in domestic medicine.

B

II. BRYOPHYTA (MOSSES AND LIVERWORTS) (92, 93, 94)

The Bryophyta or Muscineae comprise two classes, the *Hepaticae* or Liverworts, and the *Musci* or Mosses. They are distinguished from the Thallophyta by the characteristic structure of their sexual organs, ANTHERIDIA and ARCHEGONIA, which are similar to those of the Pteridophyta, the most highly developed of the Cryptogams. The Bryophyta and Pteridophyta are accordingly regarded as having been derived from a common ancestor, and, in contrast to the Thallophyta, they are referred to collectively as *Archegoniatae*.

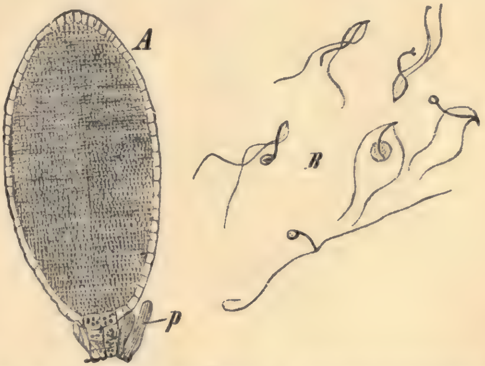


FIG. 375.—*Marchantia polymorpha*. *A*, Nearly ripe antheridium in optical section; *p*, paraphyses. *B*, Spermatozoids fixed with 1 per cent perosmic acid. (*A* × 90, *B* × 600.)

The ANTHERIDIA or male sexual organs are stalked, ellipsoidal, spherical, or club-shaped, with thin walls formed of one layer of cells and enclosing numerous small, cubical cells, each of which becomes divided diagonally into two spermatozoid mother-cells (95). At maturity the spermatozoid mother-cells separate and are ejected from the antheridium, which ruptures at the apex. By the dissolution of the enveloping walls of the mother-cells the spermatozoids are set free as short, slightly twisted filaments, terminating anteriorly in two long cilia.

The ARCHEGONIA are flask-shaped bodies with walls formed of but one layer of cells; they are sessile or shortly stalked, sometimes also somewhat sunk in the tissue, and consist of a dilated ventral portion and a neck. The ventral portion encloses a large central cell, the contents of which shortly before maturity divide into the egg-cell (Fig. 376 *A*, *o*) and the ventral-canal-cell (k''). The latter is situated at the base of the neck, just below a central row of neck-canal-cells (k'). On the maturity of the archegonium, the ventral-

and neck-canal-cells become mucilaginous and disorganised. If water is present, the cells at the apex of the neck separate (*B*) and the mucilaginous matter is discharged, and exerts through the diffusion of certain of its constituents in the water (proteid substances in *Marchantia*, cane-sugar in the case of Mosses (96)) an attractive stimulus on the spermatozoids. The spermatozoids, thus directed toward the neck of the archegonium, traverse it as far as the egg, into which one spermatozoid penetrates. The water necessary for the process of fertilisation is supplied by rain or dew. After fertilisation has been accomplished, the egg-cell divides and gives rise directly to an embryo (*C*), without first, as is usually the case in oospores, undergoing a period of rest.

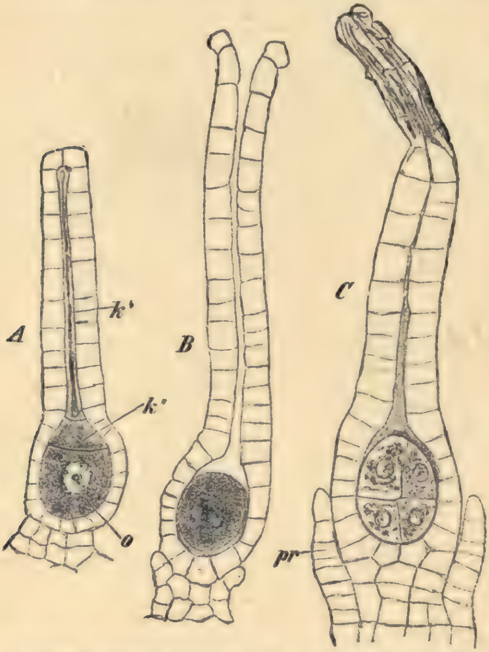


FIG. 376.—*Marchantia polymorpha*. *A*, Young, *B*, mature archegonium; *C*, fertilised archegonium, with dividing egg-cell; *k'*, neck-canal-cell; *k''*, ventral-canal-cell; *o*, egg-cell; *pr*, pseudo-perianth. (× 540.)

The Mosses as well as the Pteridophytes multiply also asexually by means of SPORES provided with cell-walls and adapted for dissemination through the air. These two modes of reproduction, sexual and asexual, occur in regular alternation, and are confined to sharply distinct generations: a sexual (gametophyte), provided with sexual organs, and an asexual (sporophyte), which produces spores. The sexual generation arises from the spore; the asexual from the fertilised egg. The number of chromosomes in the nuclei of the sporophyte is twice as great as in the nuclei of the gametophyte. The double number is acquired in the fusion of the sexual nuclei, while the reduction to one half takes place in the division of the spore-mother-cells. THIS ALTERNATION OF GENERATIONS is characteristic of all Archegoniatae.

In the development of the SEXUAL GENERATION, the unicellular spore on germinating ruptures its outer coat or EXINE, and gives rise to a germ-tube. In the case of the Hepaticae, the formation of the plant at once commences, but in most of the Musci a branched, filamentous PROTONEMA is first produced, composed of cells containing

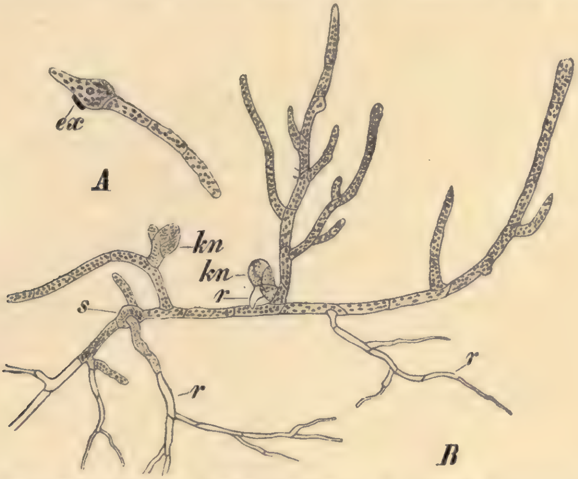


FIG. 377.—*Funaria hygrometrica.* *A*, Germinating spore ; *ex*, exine ; *B*, protonema ; *kn*, buds ; *r*, rhizoids ; *s*, spore. (After MULLER-THURGAU ; magnified.)

chlorophyll (Fig. 377 *r*). The green, filamentous protonema gives rise to branched, colourless rhizoids (*r*), which penetrate the substratum. The MOSS-PLANTS arise from buds developed on the protonema at the base of the branches. Protonema and Moss-plant, in spite of the difference in appearance between them, together represent the sexual generation. Many Liverworts possess a thallus consisting of dichotomously branching lobes, which is attached to the substratum at its base or on the under side by means of rhizoids, thus repeating the vegetative structure of many Algae (Fig. 379). In other Hepaticae, on the other hand, and in all the Musci, there exists a distinct differentiation into stem and leaves (Figs. 385, 392). In no instance, however, are true roots formed consisting of a tissue of cells, but in their stead rhizoids, consisting of colourless branching filaments, the main function of which is to attach the plant to the substratum. The Bryophytes, in this respect, differ essentially from the Pteridophytes, which are provided with true roots. The stems and leaves of Mosses are also

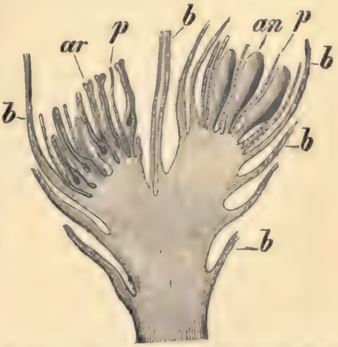


FIG. 378.—*Phascum cuspidatum.* *an*, Antheridia ; *ar*, archegonia at the apex of the bifurcated moss stem ; *b*, leaves ; *p*, paraphyses. (After HOFMEISTER, × 45.)

anatomically of a simple structure; if conducting strands are present, they are composed merely of simple elongated cells. The sexual organs are produced on the adult, sexual generation; in the thalloid forms, on the dorsal side of the thallus; in the cormophytic forms, at the apex of the stem or its branches (Fig. 378).

By the division of the fertilised egg (Fig. 376 *C*), a multicellular embryo is formed, which, by its further development, gives rise to the second or ASEXUAL GENERATION, represented by the SPOROGONIUM or the stalked MOSS CAPSULE. The sporogonium, in most cases, consists of a round or oval capsular receptacle, in whose internal tissue numerous unicellular spores are produced. At maturity the capsule opens and sets free the spores. In both the Bryophytes and Pteridophytes the spores are formed in TETRADS by the twice-repeated division of the spore-mother-cells, which previously have separated from one another and become rounded off, and represent the actual point of commencement of the sexual generation. The spore capsule has usually a shorter or longer stalk, of which the basal portion, or foot, remains in the distended venter of the archegonium, and, in consequence of the overgrowth of the underlying tissue, has the appearance of being sunk in it. Although the sporogonium constitutes a distinct asexual generation, it continues throughout its existence united with the sexual generation, and, like a semi-parasitic plant, draws from it the nourishment necessary for its development.

As shown by the occasional occurrence of intermediate structures, the antheridia and archegonia are homologous organs; the ventral-canal-cell and the neck-canal-cells of the latter represent gametes which have become functionless ([94]). Morphologically the sexual organs of Archegoniatae are most closely comparable with the plurilocular gametangia of the Phaeophyceae, while no close relation can be traced with the higher Green Algae. Further, in certain Brown Algae (*Dictyota*) a regular alternation of generations is already present; in this case, however, the gametophyte and sporophyte exhibit a similar organisation. The form of the thalloid gametophyte of the lower Liverworts shows the most marked correspondence with the Brown Algae. The sporophyte of Bryophyta has proceeded on other lines of development, but recalls the tetraspore formation in *Dictyota* by the tetrad division of the mother-cells of the asexual spores.

The two very distinct classes of Bryophytes may be briefly characterised as follows:—

1. *Hepaticae* (Liverworts).—The sexual generation, with poorly developed and generally not distinctly differentiated protonema, is either a dichotomously divided thallus or is developed as a leafy, and, with few exceptions dorsiventral shoot. In the majority of Hepaticae, in addition to spores, the capsule produces also elaters, sterile cells which, in their typical development, become greatly elongated and provided with spiral thickenings (Fig. 382 *F*). They conduct nourishment to the developing sporogenous cells, and at maturity, after the opening of the capsule, serve to separate and scatter the

spores. Only in one order, Anthocerotaceae, does the capsule have a columella, or an axial mass of sterile cells, which also conduct the metabolic products to the developing spores.

2. *Musci* (Mosses).—The protonema of the sexual generation is usually well developed and distinctly defined, and the moss plant is always segmented into stem and leaves. The leaves are arranged spirally in polysymmetrical, less frequently in bisymmetrical, rows. The capsule is always without elaters, but, except in one genus, it always possesses a columella.

CLASS I

Hepaticae (Liverworts) (97)

The Hepaticae are divided, according to the structure of the sporogonium and the segmentation exhibited by the sexual generation, into five orders: the *Ricciaceae*, *Marchantiaceae*, and *Anthocerotaceae*, comprising exclusively thalloid forms, the *Jungermanniaceae*, including both thalloid and dorsiventral foliose forms, and the *Calobryaceae*, which are radially constructed foliose forms.

Order 1. Ricciaceae (98)

Of all the Hepaticae, this order exhibits the simplest structure. The genus *Riccia* belongs to this order; its dichotomously-lobed or cleft thallus forms small rosettes, and grows on damp or marshy soil. *Riccia natans* is found floating, like Duckweed, on the surface of stagnant water. *Riccia fluitans*, on the other hand, lives wholly submerged, and has narrow, more profusely branching, thalloid segments (Fig. 379); it can, however, grow on marshy soil, and then forms flat rosettes. The Riccias are provided with fine rhizoids springing from the under side of the thallus, and possess, in addition, a row of transversely disposed ventral scales, consisting of a single layer of cells, which also function in the absorption of nourishment. Both organs are wanting in the submerged form of *Riccia fluitans*.

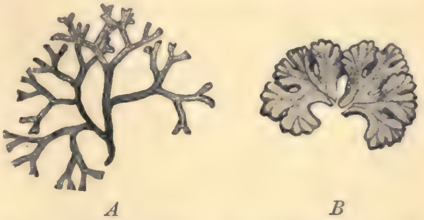


FIG. 379.—*Riccia fluitans*. *A*, Submerged floating form; *B*, land form. (Nat. size. *B*, after GOEBEL.)

The antheridia and archegonia are sunk in the surface of the upper side of the thallus. From the fertilised egg-cell is developed a spherical sporogonium which has no stalk. The wall of the sporogonium consists of a single layer of cells; it becomes disorganised during the ripening of the spores, which are eventually set free by the rupture and disintegration of the venter and the surrounding cells of the thallus.

Order 2. Marchantiaceae (99)

The Liverworts included in this order are much more highly organised, and in many genera they have a decided complicated structure. *Marchantia polymorpha*, found growing on damp soil, may serve as an example. It forms a flat deeply-lobed, dichotomously-branched thallus, about two centimetres wide, and having an inconspicuous midrib (Fig. 381 *A*, Fig. 382 *A*). From the under side of the thallus spring unicellular rhizoids, of which some have smooth walls and serve mainly to attach the thallus, while others have conical thickenings projecting into the cell-cavity; these peg-rhizoids serve for water conduction. The thallus is provided also with ventral scales, consisting of a single layer of cells. The dorsiventrality of the thallus is further shown by its complicated anatomical structure. With the naked eye it may be seen that the upper surface of the thallus is divided into small rhombic areas. Each area is perforated by a central air-pore leading into a corresponding air-chamber immediately below (Fig. 160 *A*, *B*). The lateral walls of the air-chambers determine the configuration of the rhombic areas. The air-pore in the roofing wall of each chamber is in the form of a short canal, bounded by a wall formed of several tiers of cells, each tier comprising four cells. Numerous short filaments, consisting of rows of nearly spherical cells containing chlorophyll grains, project from the floor of the air-chambers and perform the functions of assimilating tissue. Chlorophyll grains are found also in the walls and roof of the chambers, but only in small numbers. The air-chambers represent depressions in the outer surface which have become roofed over by the more rapid growth of the adjacent epidermal cells. The intensity of the illumination exercises a great influence on the formation of the air chambers; when the illumination is very weak they may not occur at all. The epidermis on the under side of the thallus is formed of one layer of cells. The tissue below the air-chamber layer is devoid of chlorophyll, and consists of large parenchymatous cells, which serve as storage cells.

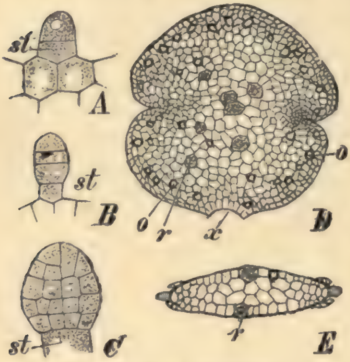


FIG. 380.—*Marchantia polymorpha*. *A*-*C*, Successive stages in the formation of a gemma; *st*, stalk-cell; *D*, surface view; *E*, transverse section of a gemma; *x*, point of attachment to stalk; *o*, oil cells; *r*, colourless cells with granular contents, from which the rhizoids will develop. (After KNY, *A*-*C* × 275; *D*-*E* × 65.)

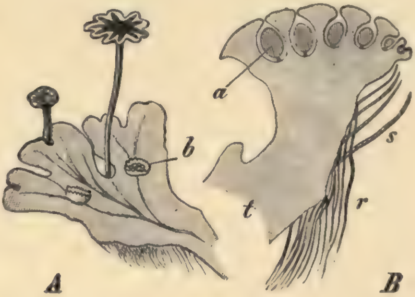


FIG. 381.—*Marchantia polymorpha*. *A*, A male plant, with antheridiophores and gemma-cups *b* (nat. size); *B*, section of young antheridiophore; *a*, antheridia; *t*, thallus; *s*, ventral scales; *r*, rhizoids. (Somewhat magnified.)

Small cup-shaped outgrowths, with toothed margins, the gemmiferous receptacles or gemma-cups, are generally found situated on the upper surface of the thallus over the midribs (Fig. 381 *b*). These contain a number of stalked gemmæ, flat, biscuit-shaped bodies of a green colour. The gemmæ arise by the protrusion and repeated division of a single epidermal cell (Fig. 380); at maturity they become detached from the stalk (at *x*, Fig. 380 *D*). They are provided with two growing points,

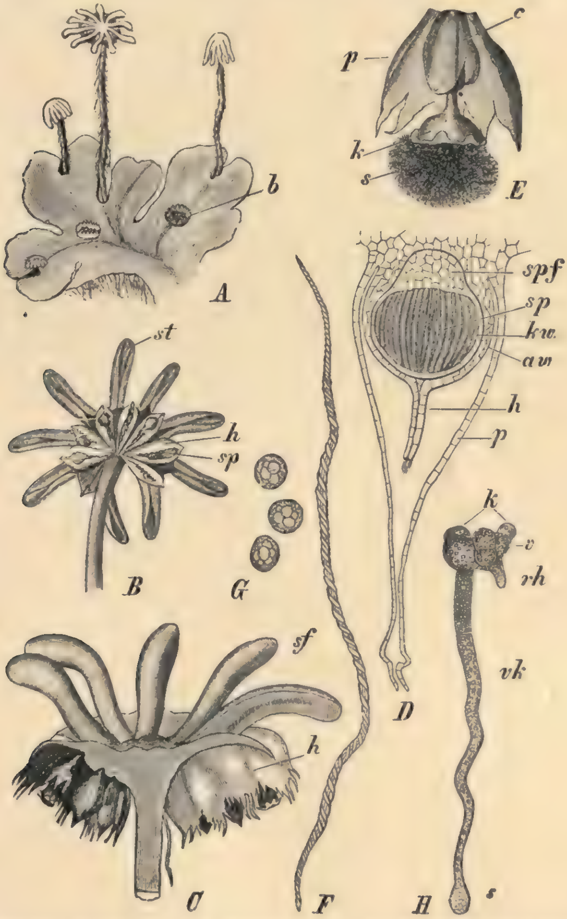


FIG. 382. – *Marchantia polymorpha*. *A*, A female plant, with four archegoniophores of different ages; *b*, gemma-cups (nat. size). *B*, under side of receptacle; *st* rays; *h*, sheath; *sp* sporogonium (×3). *C*, half of a receptacle, divided longitudinally (×5). *D*, longitudinal section of a young sporogonium; *spf*, the foot; *sp*, sporogenous tissue; *kw*, wall of capsule; *aw*, wall, and *h* neck, of archegonium; *p*, pseudo-perianth (× 70). *E*, ruptured sporogonium; *k* capsule; *s*, spores and elaters; *p*, pseudo-perianth; *c*, archegonial wall (× 10). *F* an elater. *G*, ripe spores (× 315). *H*, germinating spore (*s*); *vk*, protonema; (*k*), germ-disc, with the apical cell *v* and rhizoid *rh* (× 100). (*C*, *E* after BISCHOFF; *B*, *D*, *F-H* after KNY.)

one at each of the marginal constrictions from which their further development into new plants proceeds. On cross-section (*E*) they are seen to be composed of several layers of cells; some of the cells are filled with oil globules (*D*, *o*), while from other colourless cells rhizoids develop. Cells containing oil are also present in the mature thallus, and are of frequent occurrence in all the Hepaticae. By means of the abundantly developed gemmæ *Marchantia* is enabled to multiply vegetatively to an enormous extent.

The sexual organs, antheridia and archegonia, are borne on special erect branches of the thallus. The reproductive branches, which are contracted below into a stalk, expand above into a profusely branched upper portion. In this species, which is diœcious, the antheridia and archegonia develop on different plants. The branches producing the male organs terminate in lobed discs, which bear the antheridia on their upper sides in flask-shaped depressions, each containing an antheridium (Fig. 381 *B*). The depressions, into each of which a narrow canal leads, are separated from each other by tissue provided with air-chambers. (The structure of the antheridia and spermatozoids is illustrated by Fig. 375 and the accompanying description.)

The female branches terminate each in a nine-rayed disc (Fig. 382 *A*). The upper surface of the disc, between the rays, becomes displaced in the process of growth, and, as the archegonia are borne on these portions, they seem to arise from the under side of the disc. The archegonia are disposed in radial rows between the rays, each row being developed in a toothed lamella or sheath (Fig. 382 *B*, *C*, *h*; for structure of the archegonia see Fig 376 and description).

The fertilised egg-cell gives rise to a multicellular embryo (Fig. 376 *C*), and this, by further division and progressive differentiation, develops into a stalked oval SPOROGONIUM. The capsule of the sporogonium is provided with a wall consisting of one layer of cells, the walls of which have thickened bands, and ruptures at the apex to let free the spherical spores. The ELATERS, or elongated, spirally thickened cells formed in the capsules, between the spores, by the prolongation of definite cells, are characteristic of the Marchantias and most of the Liverworts, except the Ricciaceae. The elaters are discharged from the ruptured capsule, together with the spores, and serve for their dispersion in the same way as the capillitium of the Myxomycetes (Fig. 382, *E*, *F*, *G*). The ripe capsule, before the elongation of the stalk, remains enclosed in the archegonium wall *D*, *aw*), which, for a time, keeps pace in its growth with that of the capsule. As the stalk elongates, the archegonium wall or calyptra is broken through and remains behind, as a sheath, at the base of the sporogonium (*E*, *c*). The capsule is surrounded also by the pseudo-perianth, an open sac-like envelope which grows, before fertilisation, out of the short stalk of the archegonium (Fig. 376 *C*, *pr*; Fig. 382 *D*, *E*, *p*).

Marchantia was formerly used in the treatment of diseases of the liver; this fact explains the origin of the name Liverwort.

Order 3. Anthocerotaceae

The few forms included in this order have an irregular, disc-shaped thallus, which is firmly anchored to the soil by means of rhizoids. The cells of the thallus contain, in contrast to those of other Bryophyta, a single large chloroplast. The antheridia arise, in groups of two to four, by the division of a cell lying below the epidermis; they remain enclosed in cavities beneath the upper surface of the thallus until maturity. The archegonia are sunk in the upper surface of the thallus; after fertilisation they become covered over by a many-layered wall formed by the overarching growth of the adjoining tissue. This enveloping wall is afterwards ruptured by the elongating capsule, and forms a sheath at its base. The sporogonium consists of a swollen foot and a long, pod-shaped capsule; it has no stalk. The superficial cells of the foot grow out into rhizoid-like papillæ. The capsule splits longitudinally into two valves, and has a central hair-like columella formed of a few rows of sterile cells (Fig. 383). The columella does not extend to the apex of the capsule, but is surmounted by a narrow layer of sporogenous cells. Elaters also occur; they are multicellular, variously shaped, and often forked. The sporogonia, unlike those of all other Hepaticae, do not ripen simultaneously throughout their whole length, but from the tips downwards, and continue to elongate by basal growth after emerging from the archegonia. The wall of the sporogonium possesses stomata, which do not occur in other Liverworts; chlorophyll is present in its cells.

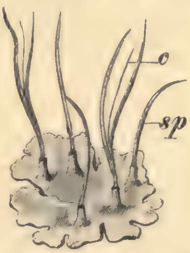


Fig. 383.—*Anthoceros laevis.* *sp*, Sporogonium; *c*, columella. (Nat. size.)

On the under side of the thallus, slit-like openings, formed by the separation of the cells, lead into cavities filled with mucilage. *Nostoc* filaments penetrate into these cavities, and develop into endophytic colonies.

Order 4. Jungermanniaceae

These are usually small forms which grow on the ground or on tree-trunks and in the tropics on the surface of living leaves. In the simplest forms of this order the thallus is broadly lobed, similar to that of *Marchantia* (*e.g. Pellia epiphylla*, frequently found on damp ground); or, like that of *Riccia fluitans*, it is narrow and ribbon-shaped, and at the same time profusely branched (*e.g. Metzgeria furcata*, Fig. 163). In the other forms, again, the broad, deeply-lobed thallus has an evident midrib, and its margins, as in the case of *Blasia pusilla* (Fig. 384), exhibit an incipient segmentation into leaf-like members. The majority of Jungerman-

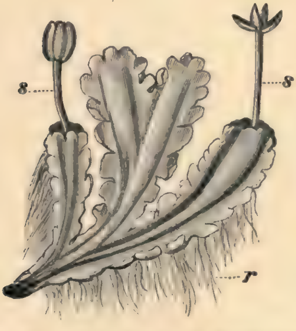


Fig. 384.—*Blasia pusilla.* *s*, Sporogonium; *r*, rhizoids. (× 2.)

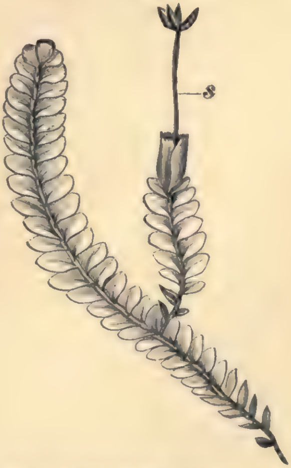


Fig. 385.—*Plagiochila asplenioides.* *s*, Sporogonium. (Nat. size.)

niaceae, however, show a distinct segmentation into stem and leaflets. The latter consist of one layer of cells without a midrib, and are inserted with obliquely directed laminæ in two rows on each flank of the stem. Some species (*e.g. Frullania Tamarisci*, a delicately branched Liverwort of a brownish colour occurring on rocks and tree-trunks) have also a ventral row of small scale-like leaves or amphigastria (Fig. 386 *a*). The dorsal leaves are frequently divided into an upper and lower lobe. In species growing in dry places, like *Frullania Tamarisci*, the lower lobe is modified into a sac, and serves as a capillary water-reservoir. The leaves regularly overlap each other; they are then said to be *succubous*, when the posterior edges of the leaves are overlapped by the anterior edges of those next below (*Frullania*, Fig. 386), or *incubous*, if the posterior edges of the leaves overlap the anterior edges of the leaves next below (*Plagiochila*, Fig. 385).

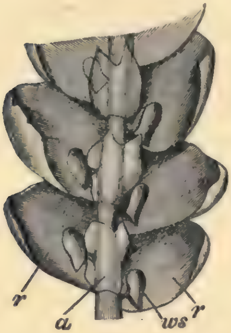


FIG. 386.—Part of a shoot of *Frullania Tamarisci*, seen from below. *r*, Dorsal leaves with the lower lobes (*ws*) modified as water-sacs; *a*, amphigastrium. (× 36.)

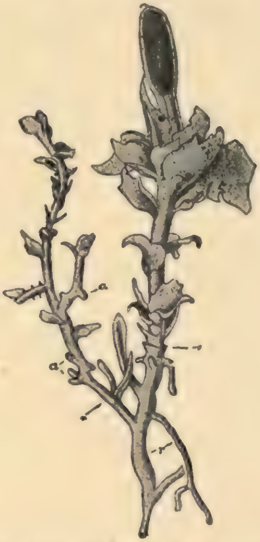


FIG. 387.—*Haplomitrium Hookeri*. *a*, origin of a new shoot *r*, rhizome; *o*, lower limit of the aerial shoot. (After GOTTSCHE.)

The branching stems of the foliose Jungermanniaceae are either prostrate or partially erect, and in consequence of the manner in which the leaves develop, present a distinctly dorsiventral appearance.

The long-stalked sporogonium is also characteristic of this order; it is already fully developed before it is pushed through the apex of the archegonial wall by the elongating stalk. It has a spherical capsule which on rupturing splits into four valves (Figs. 384, 385). No columella is formed in the capsule; but in addition to spores it always produces elaters, which, by their movements while drying, scatter the spores. The stalk of the capsule is delicate. The wall of the capsule (usually two or several cells thick) consists of cells with annular or band-like thickenings, or the walls are uniformly thickened with the exception of the outermost walls. Dehiscence is dependent on the cohesive power of the water in these cells causing the outer walls to bulge into the cavity.

According to the position of the sexual organs and sporogonium the Jungermanniaceae are divided into two groups. In the Anakrogynae the apex is not used up in the formation of the archegonia, and the sporogonia are situated on the dorsal surface and are surrounded by a sheath-like outgrowth of the thallus forming an involucre. To this group belong the thalloid forms (*Pellia*, *Metzgeria*) and others showing a transition to the frondose forms (*Blasia*). In the *Akrogynae*, on the other hand, the archegonia and the sporogonium stand at the end of the main stem or of a branch and are surrounded by a perianth formed of modified leaves. To this group belong the dorsiventral leafy forms, *e.g.* *Plagiochila* (Fig. 385), *Frullania*, and *Jungermannia*, a genus with numerous species.

Order 5. Calobryaceae (100)

This order contains only two genera, *Calobryum* occurring in the tropics and *Haplomitrium*. The single species of the latter genus *H. Hookeri* (Fig. 387) occurs in Europe, and possibly is a survival of preglacial Liverworts. The Calobryaceae differ from all other Liverworts in the radial construction of their shoot, which bears three rows of leaves. The sexual organs form terminal groups in *Calobryum*, in *Haplomitrium* they occur between the upper leaves.

CLASS II

Musci (Mosses) (101)

The profusely branched protonema of the Mosses appears to the naked eye as a felted growth of fine, green filaments (Fig. 377). The young moss plants are developed on the protonema as small buds which arise as protrusions of cells of the filament, usually from the basal cell of one of the branches. The protrusion is cut off by a transverse septum, and after the separation of one or two stalk-cells the three-sided pyramidal apical cell of the moss plant is delimited in the enlarged terminal cell (102). The moss plants are always differentiated into stem and leaf. The Mosses may be readily distinguished from the foliose Jungermanniaceae by the spiral arrangement of their small leaves, which are rarely arranged in two rows. In Mosses which have prostrate stems, the leaves, although arranged spirally, frequently assume a somewhat outspread position, and all face one way, so that in such cases a distinction between an upper and a lower side is manifested, but in a manner different from that of the Liverworts.

The STEM OF THE MOSS PLANT is formed of cells which become gradually smaller and thicker-walled towards the periphery. In the stems of many genera (*e.g.* *Mnium*, Fig. 161) there is found a central, axial strand consisting of elongated, conducting cells with narrow lumina. These strands are not as highly differentiated as the vascular bundles of Pteridophytes. They do not occur in the Sphagnaceae or Bog-mosses which grow in swampy places. The stems of the Sphagnaceae show a peculiar development of the outer cortical layers (Fig. 388 *C*). The cells in these layers are devoid of protoplasm, and are in communication with each other and the atmosphere by means of large, open pores ; to secure rigidity, they are also provided with spirally thickened walls. They have a remarkable power of capillary absorption, and serve as reservoirs for storing and conducting water.

The LEAVES of the true Mosses have, as a rule, a very simple structure. They consist usually of a single layer of polygonal cells containing chloroplasts (Fig. 63 and Fig. 100, *Funaria*), and are generally provided with a conducting bundle of elongated cells. The leaves of the Bog Mosses (Sphagnaceae) have no bundles, and instead are supplied with capillary cells for the absorption and storage of water. These cells are devoid of protoplasm, and are similar to those in the periphery of the stem, but larger and more elongated; their walls, which are perforated, are strengthened by transverse thickening bands (Fig. 388 *A*, *B*). Between them are other elongated, reticulately united cells containing chloroplasts. A similar differentiation of the leaf cells occurs in a few other Mosses (*e.g. Leucobryum vulgare*).

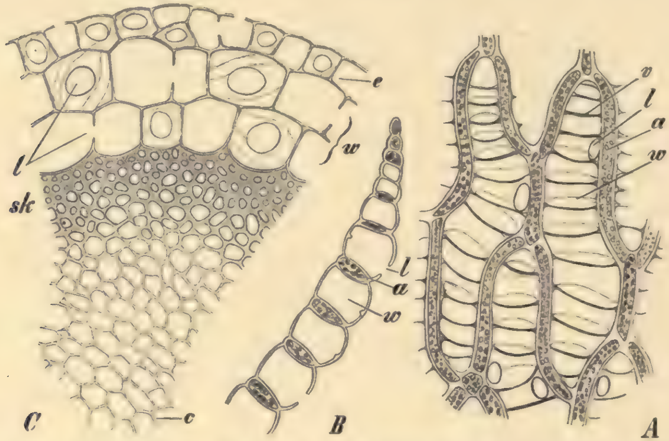


FIG. 388.—*A*, Surface view of a portion of a leaf of *Sphagnum cymbifolium* (× 300). *B*, part of a transverse section of a leaf of *Sphagnum fimbriatum*; *a*, cell containing chlorophyll; *w*, capillary cell; *v*, thickening bands; *l*, pore. *C*, part of a transverse section of the stem of *Sphagnum cymbifolium*; *c*, central cells; *sk*, sclerenchymatous cortical cells; *w*, capillary cells with pores (*l*); *e*, epidermis. (× 120.)

A more complicated structure of the leaves resulting from their adaptation to the absorption of water is exhibited by *Polytrichum commune*. In this Moss the leaves develop on their upper surface numerous, crowded, vertical lamellæ, one cell thick; these contain chlorophyll and function as assimilatory tissue, while the spaces between the lamellæ serve as reservoirs for the storage of water. In a dry atmosphere the leaves fold together, and thus protect the delicate lamellæ from excessive transpiration.

The RHIZOIDS (Fig. 395), each of which consists of a branched filament of cells, spring from the base of the stem. In structure they resemble the protonema, into which they sometimes become converted, and then give rise to new Moss plants.

The SEXUAL ORGANS are always borne in groups at the apices either of the main axes or of small, lateral branches, surrounded by their upper leaves; each group with its involucral leaves constituting a receptacle. The antheridial and archegonial receptacles are sometimes inappropriately referred to as moss flowers, but they have nothing in common with the true flowers of vascular plants; the involucral leaves, which frequently have a distinctive structure, are also known as the PERICHÆTIUM (Fig. 395). Between the sexual organs there are usually present a number of multicellular hairs or paraphyses. The moss plants may be monœcious, in which case both kinds of sexual organs are borne on the same plant either in the same or different receptacles; or diœcious, and then the antheridia and archegonia arise on different plants.

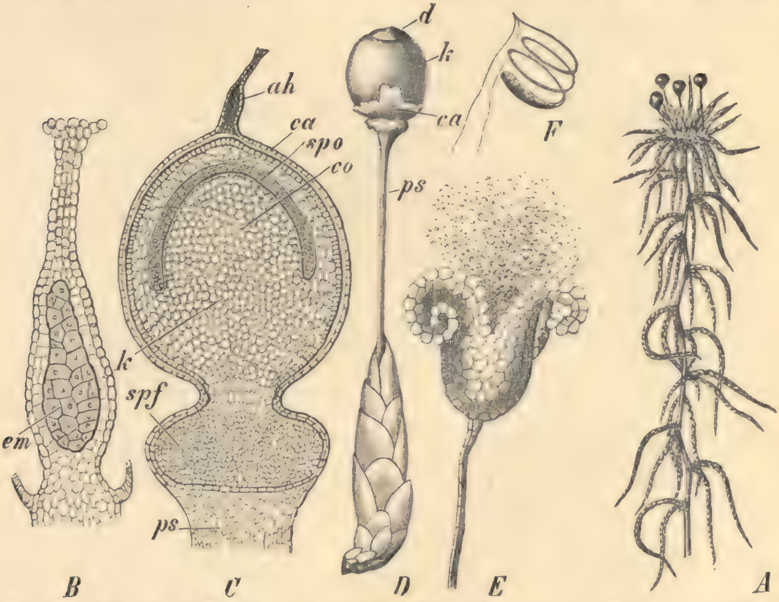


FIG. 389.—*Sphagnum fimbriatum:* *A*, A shoot with four ripe sporogonia. *Sphagnum acutifolium* *B*, Archegonium with the multicellular embryo of the sporogonium *em*; *C*, a young sporogonium in longitudinal section; *ps*, pseudopodium; *ca*, archegonial wall or calyptra; *ah*, neck of archegonium; *spf*, foot of sporogonium; *k*, capsule; *co*, columella; *spo*, spore-sac with spores; *E*, ruptured antheridium with escaping spermatozoids; *F*, single spermatozoid, highly magnified. *Sphagnum squarrosum:* *D*, A lateral shoot with a terminal sporogonium; *ca*, ruptured calyptra; *d*, operculum. (After W. P. SCHIMPER; *A*, nat. size; the other figures magnified.)

The SPOROGONIUM of the Mosses (103) develops a capsule with an axial COLUMELLA consisting of sterile tissue. The spore-sac surrounds the columella, which accumulates food material and water for the developing spores. Elaters are never formed. In the young sporogonium outside the spore-sac, a well-developed assimilating tissue is present; this is bounded by water-storage tissue and an epidermis. In most Mosses stomata are found on the lower part of the capsule. Distinctive variations in the mode of development and structure of the capsules are exhibited by the four orders of the Musci: *Sphagnaceae*, *Andreaeaceae*, *Phascaceae*, and *Bryinae*. The Sphagnaceae and Andreaeaceae are nearest to the Liverworts.

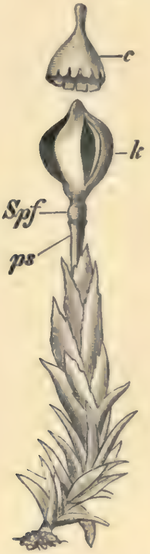


FIG. 390.—*Andreaea petrophila*. *ps*, Pseudopodium; *Spf*, foot; *k*, capsule; *c*, calyptra. (× 12.)

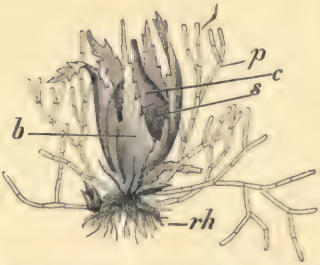


FIG. 391.—*Ephemerum serratum*. *p*, Protonema; *b*, foliage-leaf; *s*, sporogonium; *c*, calyptra; *rh*, rhizoids. (After W. P. SCHIMPER, × 200.)

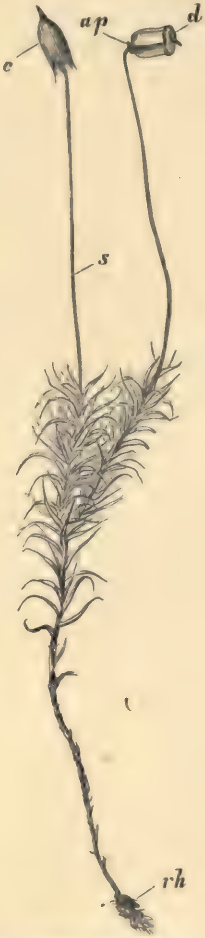


FIG. 392.—*Polytrichum commune*. *rh*, Rhizoids; *s*, seta; *c*, calyptra; *ap*, apophysis; *d*, operculum. (Nat. size.)

Order 1. Sphagnaceae (104)

The order of the Sphagnaceae, or Bog Mosses, includes only a single genus, *Sphagnum*, containing many species. The Bog Mosses grow in swampy places, and form large tussocks saturated with water. The upper extremities of the stems continue their growth from year to year, while the lower portions die away and become eventually converted into peat. Of the numerous lateral branches arising from each of the shoots, some grow upwards and form the apical tufts or heads at the summits of the stems; others, which are more elongated and flagelliform in shape, turn downwards and envelop the lower portions of the stem (Fig. 389 *A*). Every year one branch below the apex develops as strongly as the mother shoot, so that the stem thus becomes falsely bifurcated. By the gradual death of the stem from below upwards the daughter shoots become separated from it, and form independent plants. Special branches of the tufted heads are distinguishable by their different structure and colour; on these the sexual organs are produced. The male branches give rise, near the leaves, to spherical stalked antheridia, which open at the apices by means of valves; these bend back and let free the spirally twisted spermatozoids (Fig. 389 *E*, *F*). The archegonia are borne at the tips of the female branches. The sporogonium develops a short stalk with an expanded foot (*B*, *C*), but remains for a time enclosed by the archegonial wall or calyptra. Upon the rupture of the archegonium, the calyptra persists as in the Hepaticae at the base of the sporogonium. The capsule is spherical and has a dome-shaped columella, which in turn is overarched by a hemispherical

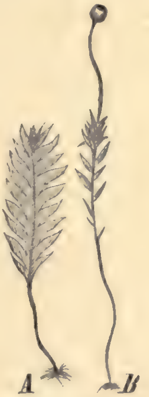


FIG. 393.—*Schistostega osmundacea*. *A*, Sterile; *B*, fertile plant. (× 5.)

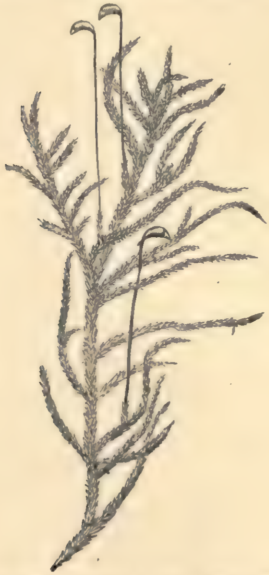


FIG. 394.—*Hypnum purum*. (Nat. size.)

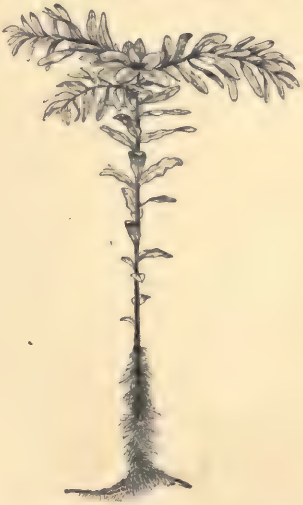


FIG. 395.—*Mnium undulatum*. Orthotropous shoot terminating in a male receptacle surrounded by involucral leaves. The lateral shoots are plagiotropous. (After GOEBEL.)

spore-sac (*spo*); it possesses an operculum, but no peristome. The ripe sporogonium, like that of *Andreaea*, is borne upon a prolongation of the stem axis, the pseudopodium, which is expanded at the top to receive the foot of the stalk. Of the peculiar structure of the leaves and stem cortex a description has already been given above. The protonema of the Sphagnaceae is in some respects peculiar. Only a short filament is formed on the germination of the spore, the protonema broadening out almost at once into a flat structure on which the young moss plants arise.

Order 2. Andreaeaceae

The Andreaeaceae comprise only the one genus *Andreaea*, small, brownish cæspitose Mosses growing on rocks. The sporogonium is also terminal in this order. The capsule, at first provided with a calyptra, splits into four longitudinal valves (schizocarpous), which remain united at the base and apex (Fig. 390). The stalk is short, and is expanded at the base into a foot (*Spf*), which in turn is borne on a pseudopodium (*ps*), a stalk-like prolongation of the stem resulting from its elongation after the fertilisation of the archegonium.

Order 3. Phascaceae

To the Phascaceae (Cleistocarpae) belong small Mosses with few leaves growing on the soil; they retain their filamentous protonemata until the capsules are ripe, and have the simplest structure of all the Mosses (Fig. 391). The capsule is terminal and has only a short stalk; it is protected by a calyptra. It does not open with a lid, but the spores are set free by the decay of its walls.

Order 4. Bryinae (105)

In this order (termed also Stegocarpae), which includes the majority of all the true Mosses, the moss fruit attains its most complicated structure. The ripe SPOROGONIUM, developed from the fertilised egg, consists of a long stalk, the SETA (Fig. 392 *s*), with a FOOT at its base, sunk in the tissue of the mother plant, and of a CAPSULE, which in its young stages is surmounted by a hood or CALYPTRA. The calyptra is thrown off before the spores are ripe. It consists of one or two layers of elongated cells, and originally formed part of the wall of the archegonium which, at first, enclosed the embryo, growing in size as it grew, until, finally ruptured by the elongation of the seta, it was carried up as a cap, covering the capsule. In the Liverworts the calyptra is, on the contrary, always pierced by the elongating sporogonium, and forms a sheath at its base. The upper part of the seta, where it joins the capsule, is termed the APOPHYSIS. In *Mnium* (Fig. 398 *A*, *ap*) it is scarcely distinguishable, but in *Polytrichum commune* it has the form of a swollen ring-like protuberance (Fig. 392, *ap*), while in species of *Splachnum* it dilates into a large collar-like structure of a yellow or red colour. The upper part of the capsule becomes converted into a lid or operculum which is sometimes drawn out into a projecting tip. At the margin of the operculum a narrow zone of epidermal cells termed the ring or ANNULUS becomes specially differentiated. The cells of the annulus contain mucilage, and by their expansion at maturity assist in throwing off the lid. In most stegocarpous Mosses the mouth of the dehisced capsule bears a fringe, the PERISTOME, consisting usually of tooth-like appendages.

The peristome of *Mnium hornum* (Fig. 398) is double; the outer peristome is formed of 16 pointed, transversely striped teeth inserted on the inner margin of the wall of the capsule. The inner peristome lies just within the outer, and consists of cilia-like appendages, which are ribbed on the inner side and thus appear transversely striped; they coalesce at their base into a continuous membrane. Two cilia of the inner peristome are always situated between each two teeth of the outer row. The cilia facilitate the dissemination of the spores by their hygroscopic movements.

The teeth and cilia of the peristome are formed in this instance of thickened portions of the opposite walls of a single layer of cells next to the operculum (Fig. 397), the teeth from portions of the external wall, and the cilia from portions of the internal walls of the same layer. On the opening of the capsule the unthickened portions of this layer break away and the teeth and cilia split apart. The transversely ribbed markings on their surface indicate the position of the former transverse walls.

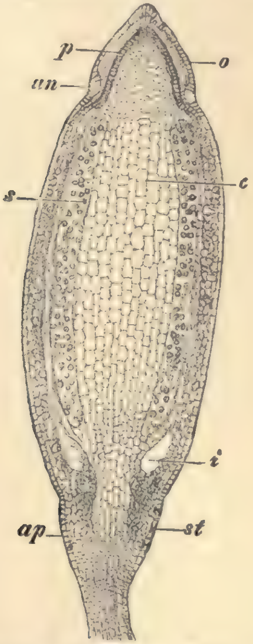


FIG. 396.—*Mnium hornum.* Median longitudinal section of a half-ripe sporogonium. *o* Operculum; *p*, peristome; *c*, columella; *s*, spore-sac containing the spores; *i*, air-space; *ap*, apophysis; *st*, stomata. (×18.)

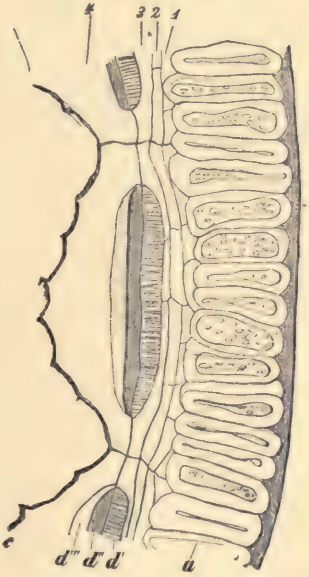


FIG. 397.—*Mnium hornum.* Transverse section through the wall of the capsule in the region of the ring. *a*, Cells of the ring; *1-4*, successive cell layers with the thickened masses of the peristome, *d′*, *d″*; *d‴*, transverse projecting ribs; *c*, the coalesced cilia. (× 240.)

The structure of the peristome varies greatly within the Bryinae. By its peculiar form and hygroscopic movements the peristome causes a gradual dissemination of the spores from the capsule.

Variations in the form of the capsule, peristome, operculum, and calyptra afford the most important means of distinguishing the different genera. The Bryinae are divided into two sub-orders, according to the position of the archegonia or of the sporogonia developed from them.

(*a*) *Bryinae acrocarpae.*—The archegonia, and consequently the sporogonia, are terminal on the main axis. *Mnium undulatum* (Fig. 395) and *hornum*, *Polytrichum commune* (Fig. 392), and *Funaria hygrometrica* are common examples. *Schistostega osmundacea*, a moss living in caves, has fertile shoots, which have spirally arranged leaves and bear stalked capsules devoid of peristomes, and also other shoots that are sterile, with two rows of leaves (Fig. 393 *A*, *B*). The protonema of this species is peculiarly constructed and gives out an emerald phosphorescent light. (Cf. Figs. 172, 214.)

(*b*) *Bryinae pleurocarpae.*—The growth of the main axis is unlimited, and the archegonia with their sporogonia arise on short, lateral branches (Fig. 394). In this group are included numerous, usually profusely branched species of large Mosses belonging to the genera *Hylocomium*, *Neckera*, and *Hypnum*, which are among the most conspicuous mosses of our woods, and also the submerged Water Moss, *Fontinalis antipyretica*.

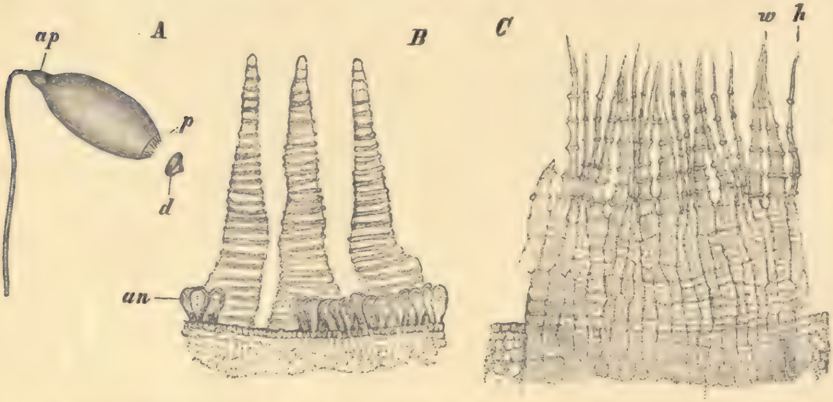


FIG. 398.—*Mnium hornum.* *A*, Capsule with upper portion of seta; *ap*, apophysis; *p*, peristome; *d*, the separated operculum. *B*, Three teeth of the outer peristome seen from the outside; *an*, annulus. *C*, inner peristome seen from the inside; *w*, broader cilia; *h*, narrower cilia. ($A \times 4$; $B, C \times 60$.)

III. PTERIDOPHYTA (VASCULAR CRYPTOGAMS) ($^{93, 106}$)

The Pteridophytes include the Ferns, Water-Ferns, Horse-tails, and Club Mosses, and represent the most highly developed Cryptogams. In the development of the plants forming this group, as in the Bryophyta, a distinct alternation of generations is exhibited. The first generation, the sexual, bears the antheridia and archegonia; the second, the asexual, develops from the fertilised egg and produces asexual, unicellular spores. On germination the spores in turn give rise to a sexual generation.

The SEXUAL GENERATION is termed the PROTHALLIUM or GAMETOPHYTE. It never reaches any great size, being at most a few centimetres in diameter; in some forms it resembles in appearance a simple, thalloid Liverwort; it then consists of a small green thallus, attached to the soil by rhizoids springing from the under side (Fig. 399 *A*). At other times the prothallium is branched and filamentous; sometimes it is a tuberous, colourless mass of tissue, partially or wholly buried in the ground, and leading a saprophytic existence, while in certain other divisions of the Pteridophyta it undergoes reduction and remains more or less completely enclosed within the spore. On the prothallia arise the sexual organs, antheridia (Figs. 404, 411), producing numerous ciliate, usually spiral spermatozoids, and archegonia (Figs. 405, 412), in each of which is a single egg-cell. As in the Mosses the presence of water is necessary for fertilisation. The spermatozoids are induced to direct their motion toward the archegonia by the excretion from the latter of a substance which diffuses into the surrounding water. In Ferns, *Salvinia*, *Equisetum*, *Selaginella*, and *Isoetes*, this substance is malic acid or one of its salts (107).

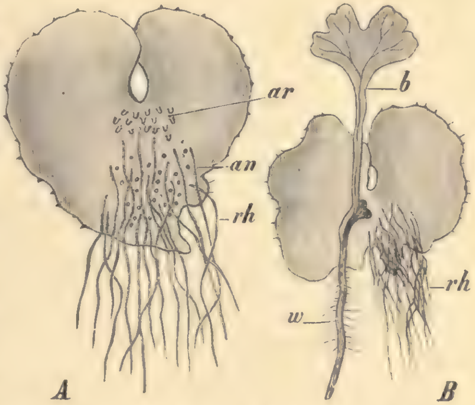


FIG. 399.—*Aspidium filix mas.* *A*, Prothallium seen from below; *ar*, archegonia; *an*, antheridia; *rh*, rhizoids; *B*, prothallium with young Fern attached to it by its foot; *b*, the first leaf; *w*, the primary root. (× circa 8.)

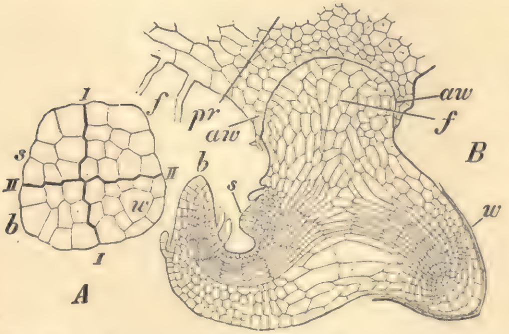


FIG. 400.—*A*, *Pteris serrulata*, embryo freed from the archegonium, in longitudinal section (after KIENITZ-GERLOFF): I, basal wall; II, transverse wall dividing the egg-cell into quadrants; rudiment of the foot *f*, of the stem *s*, of the first leaf *b*, of the root *w*; *B*, section of a further-developed embryo of *Pteris aquilina* (after HOFMEISTER); *f*, foot still embedded in the enlarged venter of the archegonium *aw*; *pr*, prothallium. (Magnified.)

After fertilisation the egg-cell develops into a multicellular embryo, which becomes the asexual generation, as in the Bryophyta.

The Bryophyta and Pteridophyta have accordingly been classed together as Embryophyta by ENGLER, and termed Embryophyta zoidiogama because the male cells are developed as spermatozoids.

The asexual generation or sporophyte is represented by a plant possessing a highly differentiated internal structure, and externally segmented into stem, leaves, and roots. In the majority of Pteridophytes (Ferns, *Equisetum*), the fertilised egg-cell, while still in the archegonium, surrounds itself with a cell wall and undergoes division, first into two cells, by the formation of a transverse or basal wall, and then into octants by two walls at right angles to each other and to the basal wall. By the further division of these eight cells a small mass of tissue is formed, and from this are developed the stem apex, the first leaf, the primary root, and an organ peculiar to the Pteridophytes, the so-called FOOT (Fig. 400 *f*). The foot is a mass of tissue, by means of which the young embryo

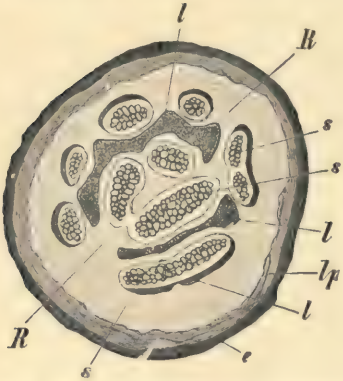


FIG. 401.—Transverse section of the rhizome of *Pteris aquilina*. *s*, Concentric vascular peripheral bundles; *l*, sclerenchymatous plates; *lp*, zone of sclerenchymatous fibres; *R*, cortex; *e*, epidermis. (× 7.)

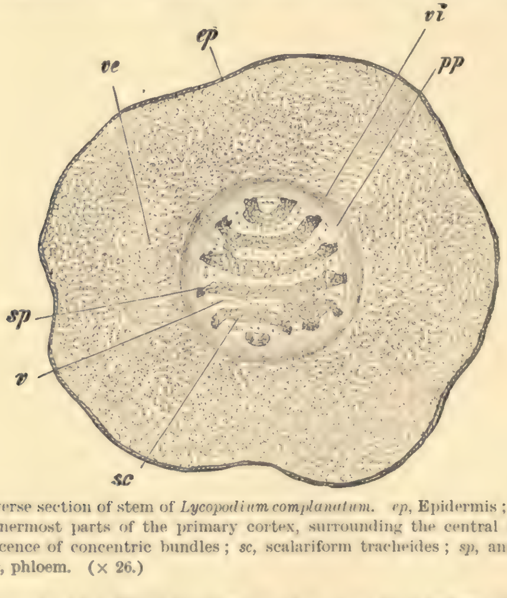


FIG. 402.—Transverse section of stem of *Lycopodium complanatum*. *ep*, Epidermis; *ve*, *vi*, *pp*, outer, inner, and innermost parts of the primary cortex, surrounding the central cylinder formed by the coalescence of concentric bundles; *sc*, scalariform tracheides; *sp*, annular and spiral tracheides; *v*, phloem. (× 26.)

remains attached to the parent prothallium and absorbs nourishment from it, until, by the development of its own roots and leaves, it is able to nourish itself independently. The prothallium then usually dies. The stem developed from the embryonic rudiment may be either simple or bifurcated, erect or prostrate; it branches without reference to the leaves, which are arranged spirally or in whorls, or occupy a dorsiventral position. Instead of rhizoids, true roots are produced, as in the Phanerogams (cf. Fig. 167). The leaves also correspond in structure with those of the Phanerogams. Stems, leaves, and root are traversed by well-differentiated vascular bundles, and the Pteridophytes are, in consequence, designated Vascular Cryptogams. The bundles of the great majority of Pteridophytes are constructed on the concentric type (cf. Fig. 401, and Fig. 125, p. 115). Secondary growth in thickness, resulting from the activity of a special cambium, occurs only occasionally in existing forms, but it was characteristic of the stems of certain extinct groups of Pteridophytes.

The SPORES are produced vegetatively in special receptacles termed SPORANGIA, which occur on the asexual generation, either on the leaves, or less frequently on the stems in the axils of the leaves. The leaves which bear the sporangia are termed SPOROPHYLLS. The sporangium consists of a wall enclosing the sporogenous tissue, the cells of which, becoming rounded off and separated from each other as spore-mother-cells, give rise each to four tetrahedral spores (spore-tetrads). The cells of the innermost layer of the sporangial wall are rich in protoplasm, and constitute the TAPETUM. This layer persists in the Lycopodineae, but in the case of the Ferns and Equisetineae the walls of the tapetal layer become dissolved. In the course of the development of a sporangium the tapetal cells then wander in between the spore-mother-cells, so that the spores eventually lie embedded in a mucilaginous protoplasmic mass, the PERIPLASM, from which they derive nourishment. The wall of the mature sporangium is formed of one or a number of layers of cells. The unicellular spores have walls composed of several coats.

The spores of the majority of the Pteridophytes are of one kind, and give rise on germination to a prothallium, which produces both antheridia and archegonia. In certain cases, however, the prothallia are diœcious. This separation of the sexes extends in some groups even to the spores, which, as MACROSPORES, developed in MACROSPORANGIA, give rise only to female prothallia; or as MICROSPORES, which are produced in MICROSPORANGIA, develop similarly only male prothallia. In accordance with this difference in the spores, a distinction may be made between the HOMOSPOROUS and HETEROSPOROUS forms of the same group; but this distinction has no systematic value in defining the different groups themselves, as it has arisen in groups in other respects quite distinct.

Compared with the Bryophyta, the asexual cormophytic generation of the Pteridophytes corresponds to the sporogonium, the prothallium on the other hand to the moss plant with its protonema; although both groups may have originated phylogenetically from a common ancestor, they have followed altogether different directions in the course of their further development. The correspondence in the structure of their sexual organs, in particular, points to the existence of a relationship between them; on the other hand, their asexual generations exhibit the greatest disagreement, so that it would not seem admissible to regard the asexual generation of the Pteridophytes as directly derived from the sporogonium of the Mosses. The asexual and sexual generations of the Archegoniatae may, however, be regarded as originally homologous.

The existing Pteridophyta are classified as follows:—

1. *Filicinae.*—Ferns. Stem simple or branched, with well-developed, alternate, often deeply divided or compound leaves. Sporangia either on the under side of the sporophylls, united in sori or free, or enclosed in special segments of the leaves.

Sub-Class 1. *Filicinae eusporangiatae.*—Ripe sporangia with firm wall composed of several layers of cells. Homosporous.
Sub-Class 2. *Filicinae leptosporangiatae.*—Ripe sporangia with walls one layer thick.

Order 1. *Filices.*—Ferns, in the narrower sense. Homosporous.
Order 2. *Hydropterideae.*—Water-Ferns. Heterosporous.

2. *Equisetinae.*—Horse-tails. Stem simple or verticillately branched, with whorled, scale-like leaves forming a united sheath at each node. Sporophylls peltate, bearing the sporangia on the under side, and aggregated into a cone at the apex of each fertile shoot.

Order 1. *Equisetaceae.*—Horse-tails. Homosporous.

3. *Lycopodinae.*—Club Mosses. Stems elongated, dichotomously branched, either forked or forming a sympodium, with leaves, in many cases greatly reduced, or shortened and tuberous with awl-shaped leaves. Sporangia arising singly in the form of firm-walled capsules either from the stem in the leaf-axils, or from the leaf-base. Tapetal cells persistent.

Order 1. *Lycopodiaceae.*—Club Mosses. Homosporous.
Order 2. *Selaginellaceae.*—Heterosporous.
Order 3. *Isoetaceae.*—Heterosporous.

There are also various fossil groups, some of which are included in the above divisions, while some form independent classes.

CLASS I.

Filicinae. Ferns (108)

The great majority of existing Pteridophytes belong to the Ferns, taking the group in a wide sense. Two sub-classes are distinguished according to the structure of the sporangia. The Eusporangiate Ferns are characterised by sporangia, the thick wall of which consists of a number of layers of cells; the sporangium originates from a group of epidermal cells together with the cells lying just below the epidermis. The Leptosporangiate Ferns on the other hand have sporangia which when mature have their wall formed of one layer of cells; each sporangium arises from a single epidermal cell. Stipules, which are found at the base of the frond in the former group, are wanting in the Leptosporangiatae. Differences also exist in the prothallus and in the structure of the sexual organs.

While in earlier geological periods the Eusporangiatae were abundantly represented, they now include only two families, each with a few genera. They appear to represent the more ancient type of Ferns and to stand nearest to the forms from which both Filicinae and Lycopodinae have been derived. The Leptosporangiatae, from which the Hydropterideae have branched off as a small group of aquatic or marsh-growing Ferns, may be derived from the Eusporangiatae. In the Hydropterideae only among Ferns the spores are differentiated into microspores and macrospores.

Sub-Class I. Eusporangiatae.

Order 1. Ophioglossaceae (109).

This family may be placed first since it appears to contain the existing forms which stand nearest to the primitive ferns. European examples are afforded by *Ophioglossum vulgatum*, Adder's Tongue (Fig. 403 *B*) and *Botrychium*, Moonwort (Fig. 403 *A*). Both have a short stem, from which only a single leaf unfolds each year. The leaves in both cases are provided with leaf-sheaths, and peculiarly divided into fertile and sterile segments. In *Ophioglossum* the sterile leaf-like segment is tongue-shaped, the fertile segment narrow and cylindrical, bearing the sporangia in two rows sunk in the tissue. The sterile portion of the leaf of *Botrychium* is pinnate, while the fertile segment is pinnately branched, and thickly beset on the inner side with large nearly spherical sporangia.

Our knowledge of the peculiar monœcious prothalli of the Ophioglossaceae is largely due to BRUCHMANN; they are long-lived, subterranean, saprophytic, tuberous bodies without chlorophyll but inhabited by a mycorhizal fungus. In *Ophioglossum* (Fig. 403 *C*) they are cylindrical and radially symmetrical, simple or branched; in *Botrychium* they are oval or heart-shaped and dorsiventral. The antheridia (Fig. 404) and archegonia (Fig. 405) are sunk in the tissue of the prothallus. The antheridium encloses a large spherical mass of spermatozoid mother-cells which are set free when mature by the swelling of the contents and the breaking down of one of the central cells of the wall. The spermatozoids have a spirally wound body and numerous cilia; a small vesicle is adherent to the spermatozoid (Fig. 404 *E*). The antheridia originate from single superficial cells (Fig. 404 *A* - *C*), as do also the archegonia (Fig. 405 *A*-*C*). The slightly projecting neck of the latter opens after the neck-canal-cell has swollen and disintegrated; the oosphere (*o*) remains in the sunken venter. In many species the embryo leads a subterranean existence for several years. The primary root is first formed and soon projects from the archegonium (Fig. 403 *C*, *K*); later the first leaf and the apical cell of the stem are differentiated. In some species of *Botrychium* the embryo forms an elongated multicellular suspensor at the end of which the proper embryonic mass is formed (110). In this an agreement with the Lycopodinae is evident (cf. Fig. 428).

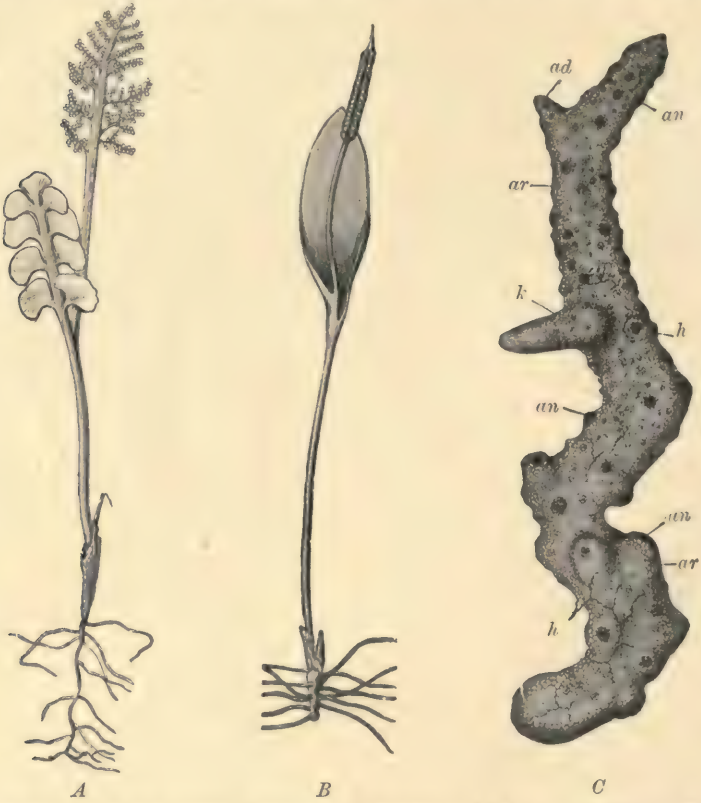


FIG. 403.—*A*, *Botrychium lunaria*. Sporophyte. (½ nat. size.) *B*, *Ophioglossum vulgatum*. Sporophyte showing the bud for the succeeding year. (½ nat. size.) *C*, *Ophioglossum vulgatum*. Prothallus. *an*, antheridia; *ar*, archegonia; *k*, young plant with the first root; *ad*, adventitious branch; *h*, fungal hyphæ. (× 15; after BRUCHMANN.)

Order 2. Marattiaceae.

This order includes a number of stately tropical Ferns with thickened tuberous stems and usually very large leaves provided with two stipules at the base. The sporangia are situated in groups (sori) on the under surface of the leaves, and are either free (*Angiopteris*), or united to form an oval capsule-like body, the chambers of which are the sporangia. The prothallium in contrast to that of the Ophioglossaceae is a green, heart-shaped thallus, resembling that of a Liverwort and growing on the surface of the soil. It is sometimes dichotomously branched. The sexual organs resemble those of the preceding order but are developed on the lower surface of the prothallus.

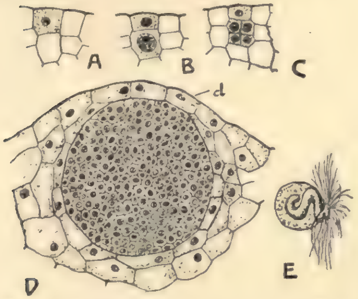


FIG. 404.—*Ophioglossum vulgatum.* *A-C*, Stages in the development of the antheridium from a superficial cell; the upper cell in *C* gives rise to the cover-cells, the lower to the mother-cells of the spermatozoids. *D*, Antheridium not yet opened; *d*, cover-cells. *E*, Spermatozoids. (After BRUCHMANN.)

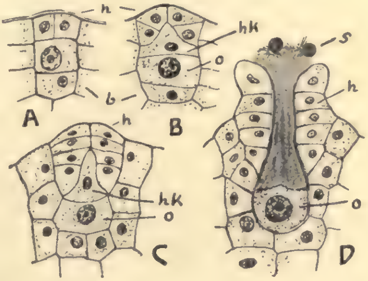


FIG. 405.—*Ophioglossum vulgatum.* *A-C*, Development of archegonium; *D*, mature opened archegonium with two spermatozoids (*s*) in front of the opening; *h*, neck-cells; *hk*, neck-canal-cells; *o*, egg-cell; *b*, basal cell. (After BRUCHMANN.)

Sub-Class II. Leptosporangiatae.

Order 1. Filices.

The Filices, or Ferns, in the narrower sense of the word, comprise a large number of genera with numerous species, being widely distributed in all parts of the world. They attain their highest development in the tropics. The Tree-Ferns (*Cyathea*, *Alsophila*, etc.), which include the largest representatives of the order, occur in tropical countries, and characterise the special family of the Cyatheaceae. The stem of a Tree-Fern (Fig. 406) is woody and unbranched; it bears at the apex a rosette of pinnately compound leaves or fronds, which are produced in succession from the terminal bud, and leave, when dead, a large leaf scar on the trunk. The stem, resembling that of a Palm in habit, is attached to the soil by means of numerous adventitious roots. The majority of Ferns, however, are herbaceous, and possess a creeping rhizome, terminating usually in a rosette of pinnate or deeply divided leaves. Such a habit and growth are illustrated by the common Fern *Aspidium filix mas*, the rhizome of which is official (Fig. 407). When young, the leaves of this Fern are coiled at the tips (Fig. 407, 1, *a*), a peculiarity common to the Ferns as a whole, and to the Water-Ferns. Unlike the leaves of Phanerogams, those of the Ferns continue to grow at the apex until their full size is attained. The leaves of the common *Polypodium vulgare* are pinnate, and spring singly from the upper side of the branched rhizome, which creeps amongst Moss or on rocks. In other cases the leaves may be simple and undivided, as in the Hart's-Tongue Fern, *Scolopendrium vulgare* (Fig. 408). In the tropics many herbaceous Ferns grow as epiphytes on forest trees.

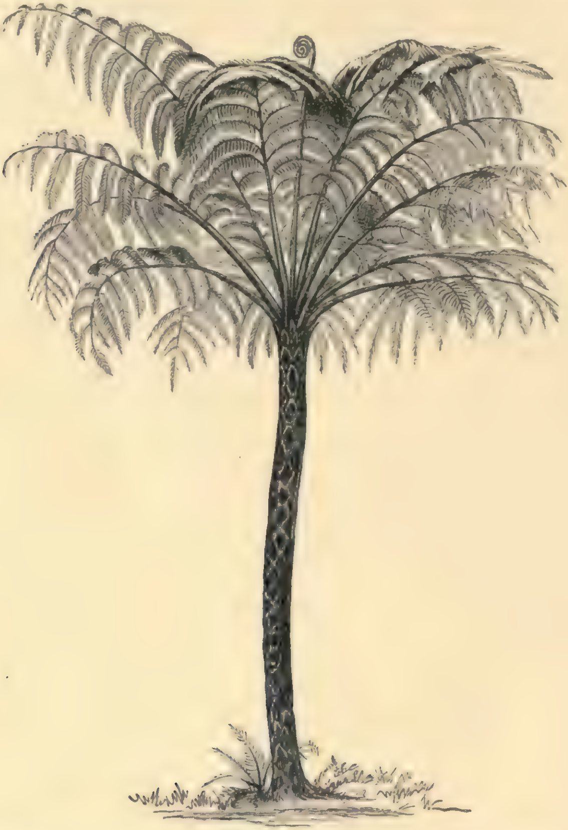


FIG. 406.—*Alsophila crinita.* A Tree-Fern growing in Ceylon. (Reduced.)

Peculiar brownish scales (paleæ, ramenta), often fringed and consisting of a single layer of cells, invest the stems, petioles, and sometimes also the leaves of most Ferns. These are morphologically trichomes.

The sporangia are generally produced in large numbers, on the under side of the leaves. The sporophylls, as a rule, resemble the sterile, foliage leaves. In a few genera a pronounced heterophylly is exhibited: thus, in the Ostrich Fern, *Struthiopteris germanica* (*Onoclea Struthiopteris*), the dark brown sporophylls are

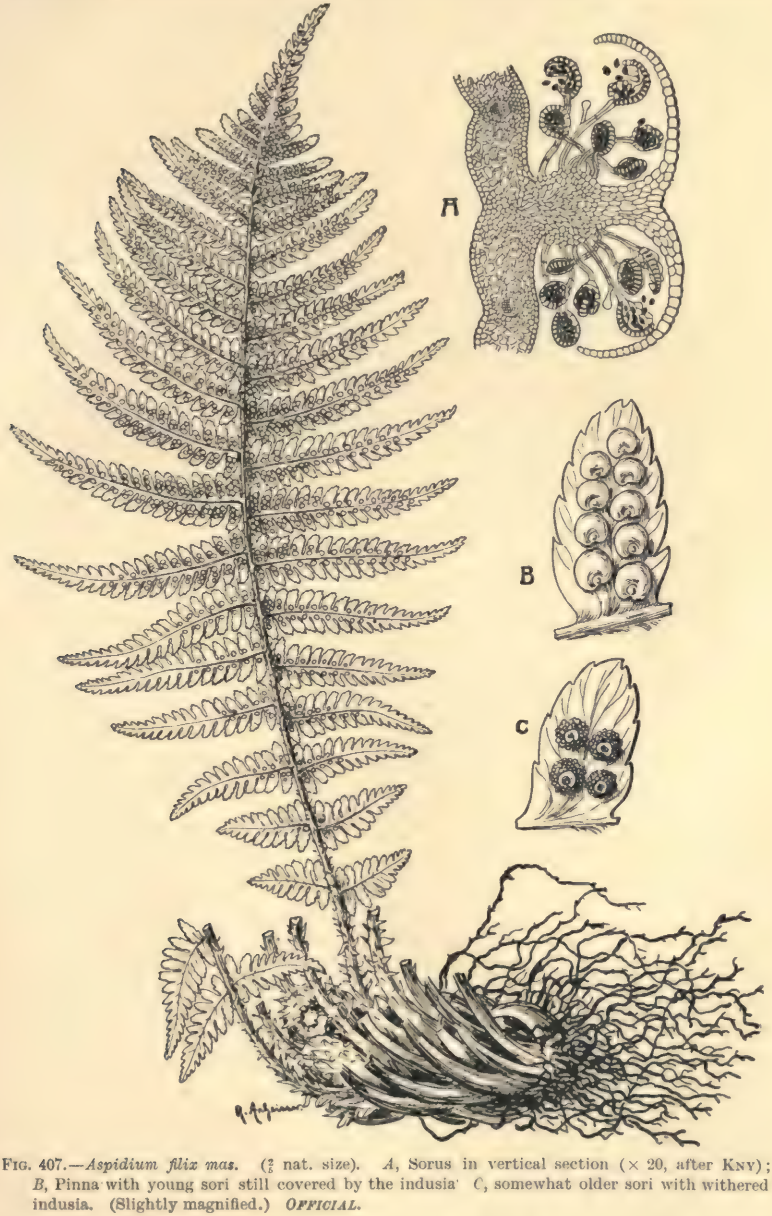


Fig. 407.—*Aspidium filix mas.* ($\frac{2}{5}$ nat. size). *A*, Sorus in vertical section (× 20, after Kny); *B*, Pinna with young sori still covered by the indusia' *C*, somewhat older sori with withered indusia. (Slightly magnified.) ***Official.***

smaller and less profusely branched, standing in groups in the centre of a rosette of large foliage leaves.

In the different families, differences in the mode of development, as well as in the form, position, and structure of the SPORANGIA are manifested.

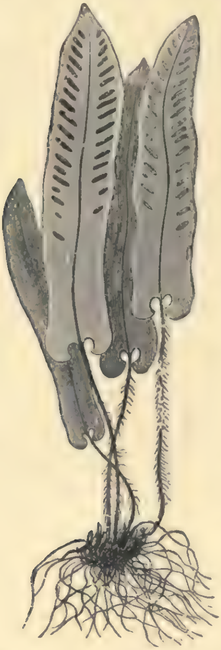


FIG. 408.—*Scolopendrium vulgare.* (¼ nat. size.)

The sporangia of the Polypodiaceae, in which family the most familiar and largest number of species are comprised, are united in groups or SORI on the under side of the leaves. They are borne on a cushion-like projection of tissue termed the RECEPTACLE (Fig. 407 *A*), and in many species are covered by a protective membrane, the INDUSIUM, which is an overgrowth of the tissue of the leaf (Fig. 407 *B*, *C*). Each sporangium arises by the division of a single epidermal cell, and consists, when ripe (Fig. 409), of a capsule attached to the receptacle by a slender multicellular stalk, containing a large number of spores. The wall of the capsule is formed of a single layer of cells. A row of cells with strongly thickened radial and inner walls, extending from the stalk over the dorsal side and top to the middle of the ventral side of the capsule, are specially developed as a ring or ANNULUS, by means of which the dehiscence of the sporangium is effected. This type of annulus is characteristic of the Polypodiaceae.

On drying of the wall of the sporangium the cohesion of the remaining water in the cells of the annulus draws in the thin outer walls of these cells; this causes the annulus to shorten and determines the dehiscence of the sporangium by a transverse slit between the broad terminal cells of the annulus. When the pull exerted by the cohesive power of the water gives way, the annulus returns by its own elasticity to its original position, thus effecting the dispersal of the spores. The sporangium remains open owing to the drying and contraction of the thin cell walls.

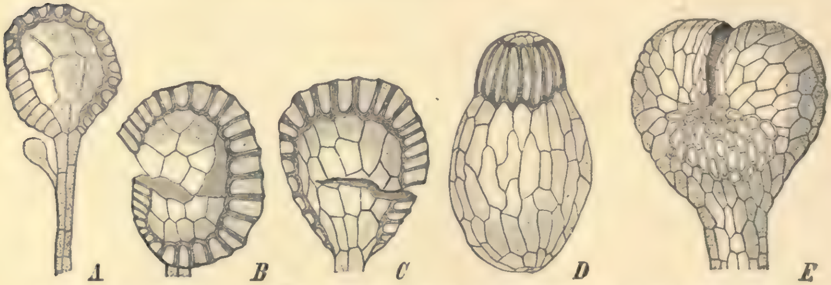


FIG. 409.—Sporangia. *A*, *Aspidium filix mas*; there is a glandular hair at the base; *B* and *C*, *Alsophila armata*, seen from the two sides; *D*, *Aneimia caudata;* *E*, *Osmunda regalis.* (*A-D* × 70 orig.; *E* × 40, after LÜRSSEN.)

The form and insertion of the sori, the shape of the indusium when present, or its absence, all constitute important criteria for distinguishing the different genera. The sori of *Scolopendrium* are linear, and covered with a lip-shaped indusium consisting of one cell-layer They are so disposed in pairs, on different sides of every two successive nerves, that they appear to have a double indusium opening in the middle. In the genus *Aspidium*, on the other hand, each sorus is orbicular in form and covered by a peltate or reniform indusium attached to the apex of the placenta; a glandular hair is frequently present on the stalk of the sporangium. The sori of *Polypodium vulgare* are also orbicular, but they have no indusia. In the common Bracken, *Pteris aquilina*, the sporangia form a continuous line along the entire margin of the leaf, which folds over and covers them with a false indusium.

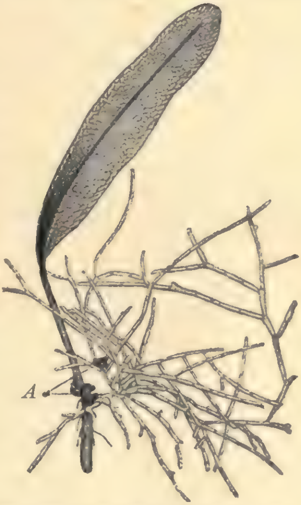


FIG. 410.—*Trichomanes rigidum*. Portion of a prothallus with an archegoniophore (*A*) to which a young plant is still attached. (After GOEBEL.)

Besides the Polypodiaceae the Ferns include other families, mainly represented in the tropics, the sporangia of which differ in the construction of the annulus and in the mechanism of their dehiscence (111). The sporangia of the Cyatheacae, to which family belong principally the tree-like Ferns, are characterised by a complete annulus extending obliquely over the apex of the capsule (Fig. 409 *B*, *C*). The Hymenophyllaceae, often growing as epiphytes on Tree-Ferns, have also sporangia, with a complete, oblique, or horizontal annulus. The sporangia of the Schizaeaceae, on the other hand, have an apical annulus (Fig. 409 *D*), while in the Osmundaceae, of which the Royal Fern, *Osmunda regalis*, is a familiar example, the annulus is represented merely by a group of thick-walled cells just below the apex of the sporangium (Fig. 409 *E*).

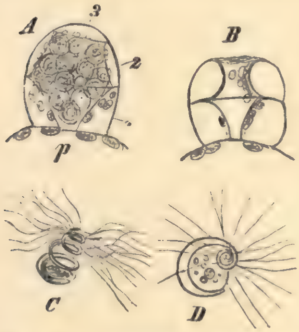


FIG. 411. — *Polypodium vulgare*. *A*, Mature, *B*, discharged antheridium; *p*, prothallium cell; 1 and 2, ring-shaped cells; 3, lid-cell; *C*, *D*, spermatozoids. (*A*, *B* × 240; C, *D* × 540.)

All the members of the Filices are homosporous. The PROTHALLIUM has usually the form of a flat, heart-shaped thallus (Fig. 399), bearing the antheridia and archegonia on the under side. In certain Hymenophyllaceae (*Trichomanes*) the prothallium is filiform and branched, resembling in structure the protonema of the Mosses, and producing the antheridia and archegonia on lateral branches (Fig. 410).

The ANTHERIDIA and ARCHEGONIA (112) are similarly constructed in nearly all Leptosporangiatae, and present differences from those of the Eusporangiate Ferns; those of *Polypodium vulgare* (Figs. 411, 412) may serve as a type. The antheridia are spherical projecting bodies (Fig. 411 *A*, *p*), arising on young prothallia by the septation and further division of papilla-like protrusions from single superficial cells. When mature, each antheridium consists of a central cellular cavity, filled with spermatozoid mother-cells, and enclosed by a wall formed of two ring-shaped cells (*A*, 1, 2) and a lid-cell (3). The spermatozoid mother-cells are produced by the division of the central cell. They are discharged from the antheridium by the pressure exerted by the swollen ring-cells, and the consequent rupturing of the lid-cell. Each mother-cell thus ejected liberates a spirally coiled spermatozoid. The anterior extremity of the spermatozoid is beset with numerous cilia, while attached to its posterior end is a small vesicle which contains a number of granules, and represents the unused remnant of the contents of the mother-cell (Fig. 411 *D*, *C*; Fig. 98 *B*).

The archegonia arise from the many-layered median portion of older prothallia. They are developed from a single superficial cell, and consist of a ventral portion, embedded in the prothallium, and a neck portion. The neck, which projects above the surface of the prothallium, consists of a wall composed of a single layer of cells made up of four cell rows (Fig. 412 *A*, *B*); it encloses the elongated neck-canal-cell. The ventral portion contains the large egg-cell and the ventral-canal-cell immediately above it. As the archegonium matures, the canal-cells become disorganised, and fill the canal with a strongly refractive mucilaginous substance. This swells on the admission of water, and, rupturing the neck at the apex, is discharged from the archegonium, which is now ready for fertilisation. The development of the embryo is represented in Fig. 400.

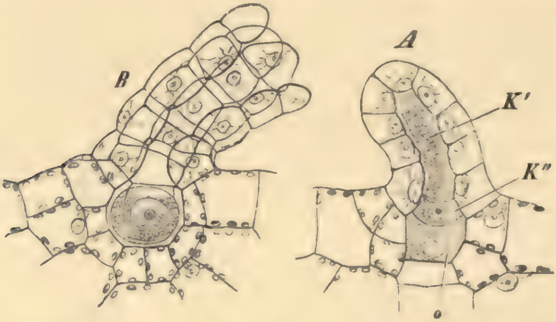


FIG. 412.—*Polypodium vulgare*. *A*, Young archegonium not yet open; *K′*, neck-canal-cell; *K″*, ventral canal-cell; *o*, egg-cell; *B*, mature archegonium, open. (× 240.)

In certain ferns the sporophyte may originate on the prothallus by a process of budding or direct vegetative growth; the sexual organs are not formed or take no part in the production of the plant (apogamy). Conversely the prothallus may arise directly, without the intervention of spores, from the tissues of the leaf (apospory) (113).

OFFICIAL.—*Aspidium filix mas*, FILIX MAS.

The long silky brown hairs from the base of the leaf-stalks of various Tree-Ferns, especially *Cibotium Barometz*, and other species of this genus, in the East Indies and the Pacific Islands, are used as a styptic (Penawar, Djambi, Pulu).

Order 2. Hydropterideae (Water-Ferns)

The Water-Ferns include only a few genera, which are more or less aquatic in habit, growing either in water or marshy places. They are all heterosporous.

The macro- and microsporangia do not develop, like those of the Filices, on the under side of the leaves, but are enclosed in special receptacles at their base, constituting sporangial fructifications or sporocarps. The wall of the sporangium, which consists of a single layer of cells, has no annulus.

The Water-Ferns are divided into two families: *Marsiliaceae*, including three genera, and *Salviniaceae*, with two genera.

Marsiliaceae.—To this family belongs the genus *Marsilia*, comprising about fifty species, of which *M. quadrifoliata* (Fig. 413) may be taken as an example. This species grows in marshy meadows, and has a slender, creeping, branched axis, bearing at intervals single leaves. Each leaf has a long erect petiole, surmounted by a compound lamina composed of two pairs of leaflets inserted in close proximity.

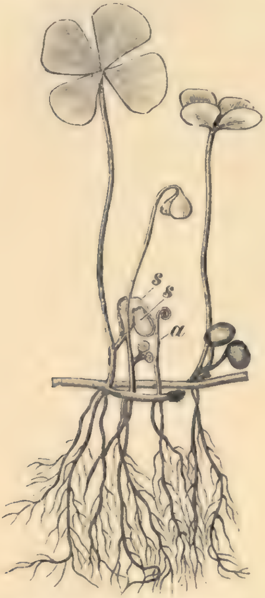


FIG. 413.—*Marsilia quadrifoliata.* *a*, Young leaf; *s*, sporocarps. (After BISCHOFF, reduced.)

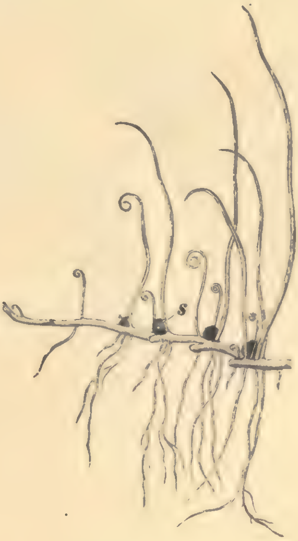


FIG. 414.—*Pilularia globulifera.* *s*, Sporocarp. (After BISCHOFF, reduced.)

The stalked oval sporocarps (*s*) are formed in pairs above the base of the leaf-stalk, or in other species they are more numerous. Each of them corresponds in development to the quadripinnate sterile lamina, but is not divided into pinnæ. The sori of sporangia are enclosed within the capsule, disposed in two rows in correspondingly arranged cavities; in the young fruit each chamber opens outwards on the ventral side by means of a narrow canal, which eventually becomes closed. The sporangia are developed originally, as in other ferns, from superficial cells, but become arched over by the surrounding tissue, and thus subsequently appear as if formed in internal chambers. As Fig. 413 shows, the young leaves, the development of which is as in the Filices, are circinate.

Pilularia also grows in bogs and marshes. It differs from *Marsilia* in its simple linear leaves, at the base of which occur the spherical sporocarps, which arise singly from the base of each sterile leaf-segment (Fig. 414).

Salviniaceae.—This family contains only free-floating aquatic plants belonging to the two genera *Salvinia* and *Azolla*. In *Salvinia natans*, as representative of the first genus, the sparingly branched stem gives rise to three leaves at each node. The two upper leaves of each whorl are oval in shape, and developed as floating foliage leaves ; the third, on the other hand, is submerged, and consists of a number of pendent, filamentous segments which are densely covered with hairs, and assume the functions of the missing roots. The sporocarps have an entirely different mode of development from those of the Marsiliaceae ; they are spherical, and are borne in small groups on the submerged leaves at the base of the filamentous segments (Fig. 415 A). The sporangia are produced within the sporocarp from a column-like receptacle, which corresponds in origin to a modified leaf-segment. The envelope of the sporocarp is equivalent to an indusium ; it arises as a new growth in the form of an annular wall, which is at first cup-shaped, but ultimately closes over the receptacle and its sorus of sporangia.

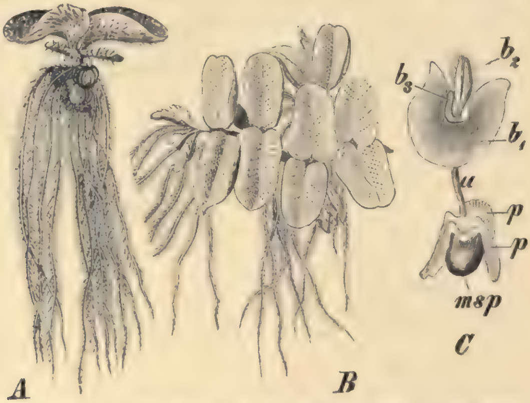


Fig. 415.—*Salvinia natans.* *A*, Seen from the side ; *B*, from above (after Bischoff, reduced) ; *C*, an embryonic plant ; *msp*, macrospore ; *p*, prothallium ; *a*, stem ; b_1, b_2, b_3, the first three leaves ; b_1, the so-called scutiform leaf. (After Pringsheim, × 15.)

The second genus, *Azolla*, is chiefly tropical, represented by small floating plants, profusely branched, and beset with two-ranked closely crowded leaves. Each leaf consists of two lobes, of which the upper floats on the surface of the water, while the lower is submerged, and assists in the absorption of water. A small cavity enclosed within the upper lobe, with a narrow orifice opening outwards, is always inhabited by filaments of an Alga (*Anabaena*). From the fact that hairs grow out of the walls of the cavity between the algal filaments, the existence of a symbiotic relation between the two plants would seem to be indicated. *Azolla*, unlike *Salvinia*, possesses true roots developed from the under side of the stem. The sporocarps are nearly spherical, and produced usually in pairs on the under side of the first leaf of some of the lateral branches.

In the structure of the sporangia and spores, and in the development of the prothallia, the Hydropterideae differ in many respects from the Filices. These differences may be best understood on reference to *Salvinia natans* (114) as an example. The sporocarps contain either numerous microsporangia or a smaller number of macrosporangia (Fig. 416 *A*, *ma*, *mi*). In structure both forms of sporangia resemble the sporangia of the Leptosporangiate Ferns; they are stalked, and have, when mature, a thin wall of one cell-layer but no annulus (*B*, *D*). The MICROSPORANGIA enclose a large number of microspores, which, as a result of their development in tetrads from the mother-cells, are disposed in groups of four (*C*), and embedded in a hardened frothy mass filling the cavity of the sporangium. This frothy interstitial substance is derived from the tapetal cells, which gradually lose their individuality and wander in between the spore mother-cells.

The microspores germinate within the microsporangium, which does not open; each germinating microspore puts out a short tubular male prothallium, which pierces the sporangial wall. The antheridium is developed in this by successive divisions (Fig. 417). Each antheridium produces four spermatozoids, which are set free by the rupture of the cell-walls. Although the whole male prothallium is thus greatly reduced, it nevertheless exhibits in its structure a resemblance to the prothallia of the Filices.

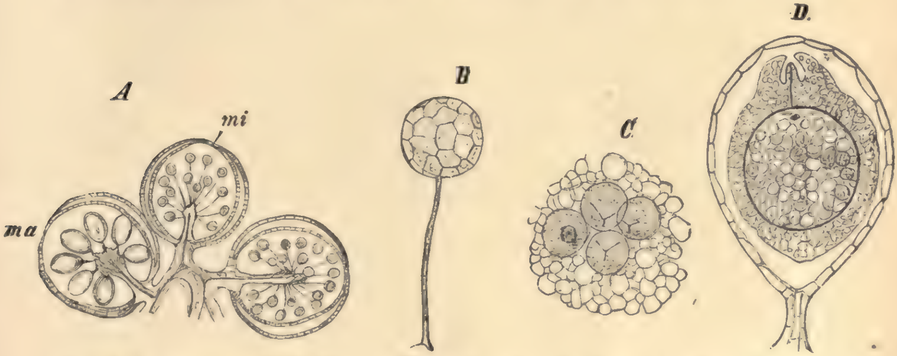


FIG. 416.—*Salvinia natans*. *A*, Three sporocarps in median, longitudinal section; *ma*, macrosporocarp; *mi*, microsporocarp (× 8); *B*, a microsporangium (× 55); *C*, portion of the contents of a microsporangium, showing four microspores embedded in the frothy interstitial substance (× 250); *D*, a macrosporangium and macrospore in median longitudinal section (× 55).

The MACROSPORANGIA are larger than the microsporangia, but their walls consist similarly of one cell-layer (Fig. 416 *D*). Each macrosporangium produces only a single large macrospore, which develops at the expense of the numerous spores originally formed. The macrospore is densely filled with large angular proteid grains, oil globules, and starch grains; at its apex the protoplasm is denser and contains the nucleus; the membrane of the spore is covered by a dense brown exinium, which in turn is enclosed in a thick frothy envelope, the perinium, investing the whole spore and corresponding to the interstitial substance of the microspores, and also formed from the dissolution of the tapetal cells. The macrospore remains within the sporangium, which is eventually set free from the mother plant and floats on the surface of the water. On the germination of the macrospore, a small-celled female prothallium is formed by the division of the denser protoplasm at the apex, while the large underlying cell does not take part in the division, but from its reserve material provides the developing prothallium with nourishment. The spore wall splits into three valves, the sporangial wall is ruptured, and the green prothallium protrudes as a small saddle-shaped body. On it three archegonia are produced, but only the fertilised egg-cell of one of them develops into an embryo, whose foot, remaining for a time sunk in the venter of the archegonium, finally ruptures it (Fig. 418). The first leaf of the germ plant is shield-shaped (Fig. 415 *C*).

The development of *Azolla* ([115]) proceeds in a similar manner, but the sporangia and spores exhibit a number of distinctive peculiarities. The numerous spores of the microsporangia are aggregated into several nearly spherical balls or massulæ, formed from the interstitial substance derived from the protoplasm of the tapetal cells. Each massula, enclosing a number of spores, is beset externally with barbed, hook-like outgrowths of the interstitial substance (glochidia). On the rupture of the sporangia the massulæ are set free in the water, and are carried to the macrospores, to which they become attached. A sporocarp contains one macrosporangium, in which only a single macrospore comes to maturity; in the course of its development it supplants all the other sporogenous cells, and finally the sporangial wall itself becomes flattened against the inner wall of the sporocarp, frequently undergoing at the same time partial dissolution. The macrospore is enveloped by a spongy perinium whose outer surface exhibits numerous depressions and protuberances prolonged into filaments. At the apex of the spore the perinium expands into three pear-shaped appendages, while the upper part of the ruptured

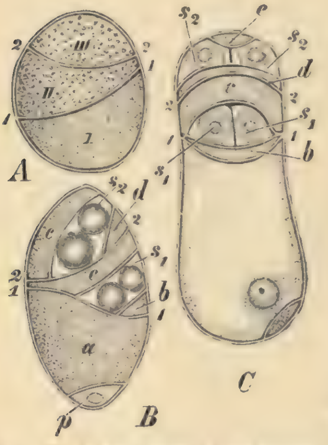


FIG. 417.—*Salvinia natans.* Development of the male prothallium. *A*, Division of the microspore into three cells *I-III* (× 860); *B*, lateral view; *C*, ventral view of mature prothallium (× 640). Cell *I* has divided into the prothallium cells *a* and *p*; cell *II*, into the sterile cells *b*, *c*, and the two cells s_1, each of which has formed two spermatozoid mother-cells; cell *III*, into the sterile cells *d*, *e*, and the two cells s_2. The cells s_1s_1 and s_2s_2 represent two antheridia; the cells *b*, *c*, *d*, *e* their wall-cells. (After BELAJEFF.)

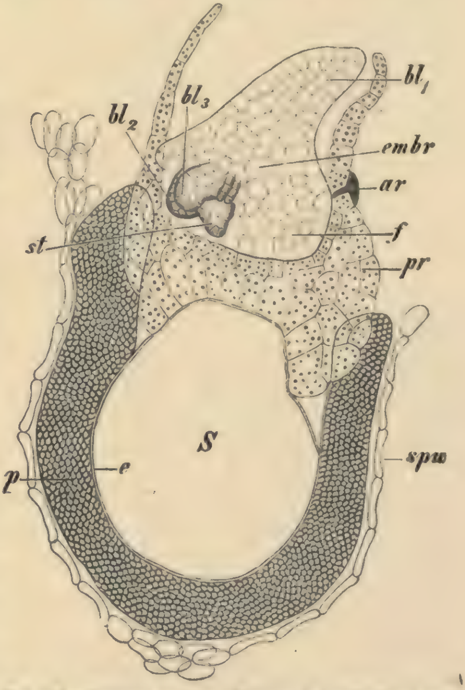


FIG. 418.—*Salvinia natans.* Embryo in longitudinal section; *pr*, prothallium; *S*, spore-cell; *e*, exinium; *p*, perinium; *spw*, sporangial wall; *ar*, archegonium; *embr*, embryo; *f*, foot; bl_1, bl_2, bl_3, the first three leaves; *st*, apex of stem. (After PRINGSHEIM, × 100.)

sporangium remains attached to the spore in the form of an umbrella-like expansion. The formation of the prothallia is effected in essentially the same way as in *Salvinia*, except that only one antheridium with eight spermatozoids arises on each of the small male prothallia protruding from a massula.

The sporocarps of the Marsiliaceae have a more complicated structure: those of *Pilularia globulifera* are divided into four chambers, each with a single sorus; in *Marsilia* they enclose numerous sori (14-18) disposed in two rows. The sori in both genera contain both micro- and macrosporangia, while those of the Salviniaceae always consist of only one kind of sporangium.

In the case of the Marsiliaceae the prothallia are even more reduced, but otherwise their mode of development is very similar. Each of the minute female prothallia formed at the apices of the macrospores produces a single archegonium.

CLASS II

Equisetinae (Horse-tails) (116)

The Equisetinae, which form an entirely independent class, include only the one genus *Equisetum*, comprising 20 species, found widely distributed over the whole world. Developed partly as land, partly as swamp plants, they may always be distinguished by the characteristic structure and habit of the asexual generation. They have a branching, underground rhizome on which arise erect, aerial haulms, usually of annual growth. The rhizome of the common Horse-tail, *Equisetum arvense*, develops also short tuber-like branches which function as reservoirs of reserve material and hibernating organs (Fig. 420). The aerial haulms remain either simple, or they give rise to branch whorls, and these in turn to whorls of a higher order. All the axes are formed of elongated internodes; they have a central pith-cavity and a peripheral series of smaller air channels. The collateral vascular bundles form a single circle, as seen in transverse section (Fig. 419).

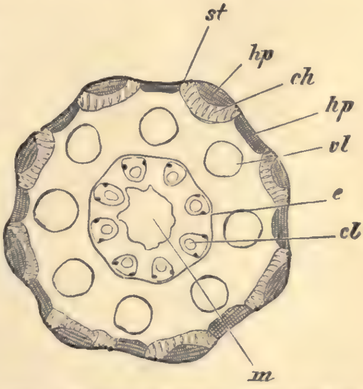


Fig. 419.—*Equisetum arvense*. Transverse section through the stem. *m*, lysigenic medullary cavity; *e*, endodermis; *cl*, carinal canals in the collateral bundles; *vl*, vallecular cavities; *hp*, sclerenchymatous strands in the furrows and ridges; *ch*, tissue of the primary cortex containing chlorophyll; *st*, rows of stomata. (× 11.)

The leaves of the Equisetinae, both in their structure and in the manner of their arrangement on the stem, are also characteristically developed. At each node is borne a whorl of scale leaves pointed at the tips, and united below into a sheath closely enveloping the base of the internode. The leaves of the successive whorls alternate regularly with each other. The lateral branches are developed in the axils of the scale leaves, but not having space to grow upwards they pierce the narrow sheath. As a result of the reduction of the leaf laminæ, the haulms themselves assume the function of assimilation, and for that purpose their cortical tissue under the epidermis is provided with chlorophyll.

The SPORANGIA are borne on specially shaped leaves or sporophylls. Like the scale leaves the sporophylls are developed in whorls, but are closely aggregated at the tips of the erect fertile shoots into a cone (Fig. 420), which is sometimes spoken of as a flower, from the correspondence in its structure to the male flower

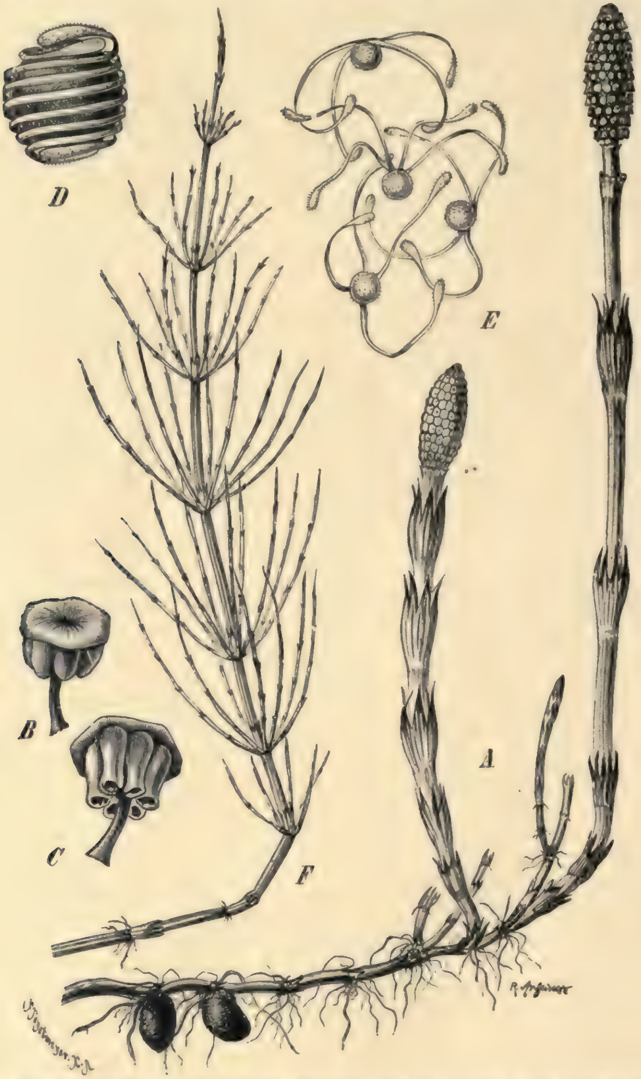


FIG. 420.—*Equisetum arvense.* *A*, Fertile shoot, springing from the rhizome, which also bears tubers; the vegetative shoots have not yet unfolded. *F*, Sterile vegetative shoot. *B*, *C*, Sporophylls bearing sporangia, which in *C* have opened. *D*, Spore showing the two spiral bands of the perinium. *E*, Dry spores showing the expanded spiral bands. (*A*, *F*, ½ nat. size. *B*, *C*, *D*, *E*, enlarged.)

of the Conifers. The lowest whorl is sterile, and forms a collar-like protuberance. The sporophylls (Fig. 420 *B*, *C*) are stalked and have a peltate expansion, on the under side of which are borne the sac-like sporangia (5-10). In the young sporangium the sporogenous tissue is surrounded by a wall consisting of several cell layers, but eventually the tapetal cells of the inner layer become disorganised, and their protoplasm penetrates between the developing spores. At maturity the wall of the sporangium consists only of the outermost of the original layers, the cells of which are provided with annular and spiral thickenings ; the sporangia thus resemble the homologous pollen-sacs of Phanerogams. The dehiscence is determined by the cohesive force of the diminishing amount of water in the cells of the outer layer and the contraction of the thin parts of the cell walls on drying (117). The sporangia split longitudinally, and set free a large number of green spores, which are nearly spherical in shape, and have peculiarly constructed walls. In addition to the intine and exine, the spores are overlaid with a perinium formed from the protoplasm of the tapetal cells, and consisting of two spiral bands which are attached to the spores only at their point of intersection (Fig. 420 *D*). On drying, the spiral bands loosen and become uncoiled ; when moistened they close again around the spore. By means of their hygroscopic movements they serve to hook together the spores, and in this way assure the close proximity of the unisexual prothallia which the latter produce (Fig. 420 *E*).

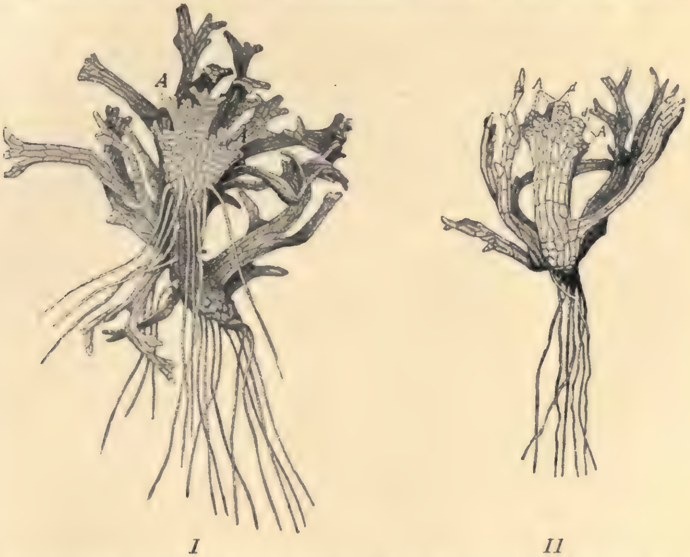


FIG. 421.—*Equisetum pratense.* *I*, Female prothallium from the under surface, showing the archegonia (*A*). *II*, Male prothallium with antheridia (*A*) ; *d*, cover cells of antheridia. (*I* × 17, *II* × 12. After GOEBEL.)

In certain species some of the aerial haulms always remain sterile, branching profusely, while others which produce the terminal cones either do not branch at all, or only at a later stage, and then sparingly. This distinction between the sterile and fertile haulms is most marked in *Equisetum arvense* and *Equisetum Telmateja*, in both of which the fertile shoots are entirely unbranched, and terminate in a single cone (Fig. 420). Resembling in their mode of life a parasite upon the rhizome, they are otherwise distinguished from the vegetative haulms by their lack of chlorophyll and their light yellow colour.

Equisetum giganteum, growing in South America, is the tallest species of the genus; its branched haulms, supported by neighbouring plants, attain a height of over twelve metres, and are about two cm. in diameter.

The spores are all of one kind, and on germination give rise to thalloid PROTHALLIA, which are generally diœcious (Fig. 421). The female prothallia are larger than the male, and, branching profusely, are prolonged into erect, ruffled lobes at whose base the archegonia are produced. In structure the archegonia resemble those of the Ferns, but the upper cells of the four longitudinal rows of cells constituting the neck are more elongated and, on opening, curve strongly outwards. The first leaves of the embryo are arranged in a whorl and encircle the apex of the stem. The growth of the embryo is effected by the division of a three-sided apical cell (Figs. 164, 165).

The outer epidermal walls of the stem are more or less strongly impregnated with silica. In *Equisetum hiemale*, and to a less degree in *Equisetum arvense*, the silicification of the external walls is carried to such an extent that they are used for scouring metal utensils and for polishing wood.

Poisonous substances are formed in some species of *Equisetum*, and hay with which the shoots are mixed is injurious to cattle.

CLASS III

Lycopodinae (Club Mosses)

To the Lycopodinae belong, as their most important and widely distributed genera, *Lycopodium*, *Selaginella*, and *Isoetes*. They are distinguished from the other Pteridophyta, of which they resemble most nearly the Eusporangiate Filices, by their general habit and the mode of their sporangial development.

Unlike the fertile leaves of the Filicinae and Equisetinae, which always bear numerous sporangia, the sporophylls of the Lycopodinae produce the sporangia singly, at the base of the leaves or in their axils. Although in many cases scarcely distinguishable from the sterile leaves, the sporophylls are frequently distinctively shaped, and, like those of *Equisetum*, aggregated at the ends of the fertile shoots into terminal spike-like cones or flowers. Compared with the leaves, the sporangia are relatively large. They are developed in the same way as those of the Eusporangiate Filices and Equisetinae, from a projecting group of cells derived from the epidermis and the underlying tissue; while in the other Pteridophyta the sporangia are developed from a single epidermal cell. The innermost layer of the sporangial wall, the tapetal layer, is not absorbed. The sporangia have no annulus. Except in the case of *Isoetes*, whose spores become free by the decay of the sporangial wall, they dehisce by longitudinal slits, which divide the sporangia into two or more valves; the slits occur where rows of cells of the wall have remained thin (117). The sporangia of *Lycopodium* are homosporous; those of other Lycopodinae heterosporous. The heterosporous forms produce only greatly modified and reduced prothallia; in the genus *Lycopodium*, on the other hand, the prothallia are well developed, and resemble those of the Ophioglossaceae. In the development of their sexual generation the heterosporous Lycopodinae resemble in many respects the heterosporous Hydropterideae.

The dichotomous branching of the stems and roots is characteristic of this class (Figs. 18, 19).

Order 1. Lycopodiaceae (118)

The numerous, widely distributed species of the genus *Lycopodium* (Club Moss) are for the most part terrestrial plants; in the tropics epiphytic forms also occur. In *Lycopodium clavatum*, one of the commonest species, the stem, which is thickly

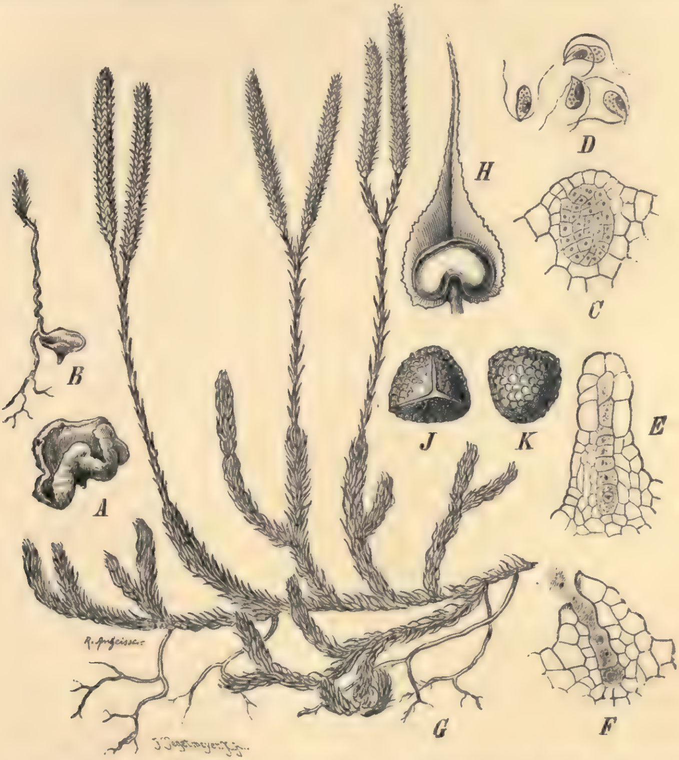


FIG. 422.—*Lycopodium clavatum*. *A*, Old prothallus. *B*, Prothallus with young plant attached. *C*, Antheridium in vertical section. *D*, Spermatozoids. *E*, Young archegonium, the neck still closed. *F*, Open archegonium ready for fertilisation. *G*, Plant bearing cones (½ nat. size). *H*, Sporophyll with an opened sporangium. *J*, *K*, Spores from two points of view. (*A-F*, after BRUCHMANN.)

covered with small, awl-shaped leaves, creeps along the ground ; it branches dichotomously, and gives rise to ascending lateral branches, while from the under side spring the dichotomously branched roots (Fig. 422). The cone-like flowers, consisting of the closely aggregated sporophylls, are situated in groups of two or more at the ends of the forked erect shoots. The sporophylls are not like the sterile leaves in shape ; they are broader and more prolonged at the tip ; each bears a large reniform sporangium on the upper side at the base. The sporangium opens into two valves by a transverse slit, and lets free numerous minute spores (Fig. 422 *H*). *Lycopodium Selago* differs in habit from the other species ; its bifurcately branched stems are all erect, and the flower-cones are not distinct from the vegetative region of the fertile shoots.

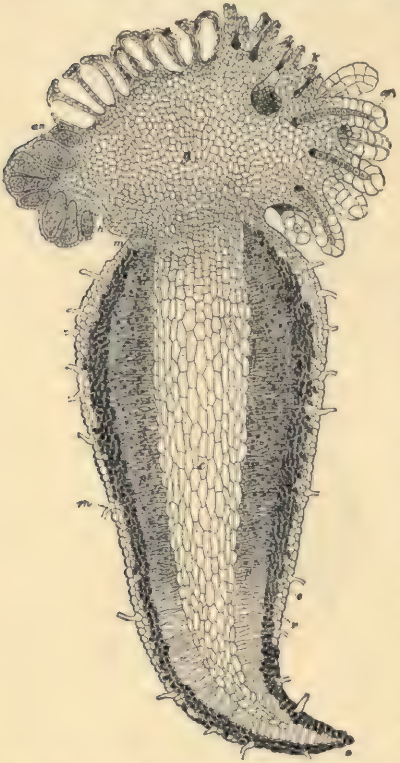


FIG. 423.—*Lycopodium complanatum.* Prothallus with antheridia (*aa*), archegonia (*ar*), and a young embryo (*k*). (After BRUCHMANN. × 26.)

The spores of the Lycopodiums are all of one kind, and in consequence of their formation in tetrads are of a tetrahedral though somewhat rounded shape. The exine is covered with a reticulate thickening (Fig. 422 *J*, *K*).

The mode of germination and development of the sexual generation have as yet been determined only for a few species. The prothallia of *Lycopodium clavatum* and the closely related *L. annotinum* are small white tuberous structures, which live as subterranean saprophytes. At first top-shaped, they become converted by the continued marginal growth into cup-shaped lobed bodies, which may attain a size of two centimetres. Long rhizoids spring from the lower surface, while the upper surface bears numerous antheridia and archegonia. In *L. complanatum* (Fig. 423) the subterranean prothalli are turnip-shaped, in *L. Selago* rounded or elongated and cylindrical. The prothalli of the latter may be developed on the surface of the soil, in which case they are green. In the case of *L. inundatum*, the prothalli of which are found on damp peaty soil, and in the tropical *L. cernuum*, with erect profusely branched shoots, the prothallia are poor in chlorophyll and are attached to the soil by rhizoids ; they have the form of small, half-buried, cushion-like masses of tissue, which give rise to green aerial thalloid lobes. The archegonia occur at the base of these lobes, the antheridia also on their surface.

The prothallia are all monœcious. The antheridia are somewhat sunk in the tissue (Fig. 422 *C*) and enclose numerous spermatozoid mother-cells, in which small biciliate spermatozoids are formed. The archegonia (Fig. 422 *E*, *F*) are constructed like those of the Ferns, but have a shorter neck, whose upper cells become disorganised on opening. The number of neck-canal-cells differs in the various species (1, 3, 5, or 6-10).

The embryonic development agrees closely with that of *Selaginella* (Fig. 428). A SUSPENSOR is developed; it is not, however, laterally inserted, but occurs, on the contrary, at the foot end of the embryo, or between the foot and the apex of the stem.

The spores of *Lycopodium clavatum* and other species are sometimes used in pharmacy.

Order 2. Selaginellaceae (119)

To this order belongs the genus *Selaginella*, represented by numerous and for the most part tropical species. They have, as a rule, profusely forked, creeping, and sympodially branched stems, but occasionally erect, branched stems; some form moss-like beds of vegetation; others, climbing on adjacent plants, possess stems several metres long. In general the Selaginellas are similar in habit to the Lycopodiums. They have small, scale-like leaves which usually exhibit a dorsi-ventral arrangement, such as is shown, for example, in the alpine *Selaginella helvetica* (Fig. 424), the stem of which bears two rows of small dorsal or upper leaves, and opposite to them two rows of larger, ventral or under leaves. The development of a small, membranous ligule at the base of the leaves, on their dorsal side, is characteristic of the Selaginellas. The rhizophores(120) are organs that are peculiar to the plants of this order; they are cylindrical, leafless, shoot-like structures, which arise exogenously, usually in pairs, from the stem at a bifurcation

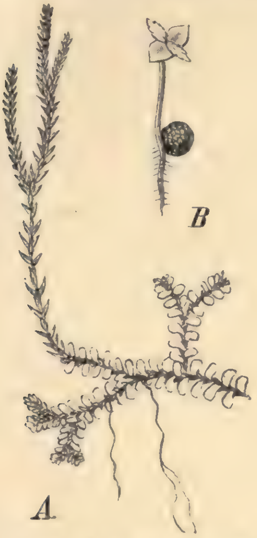


FIG. 424.—*A*, *Selaginella helvetica* (from nature, nat. size). *B*, *Selaginella denticulata*, embryonic plant with macrospore still attached. (After BISCHOFF, magnified.)

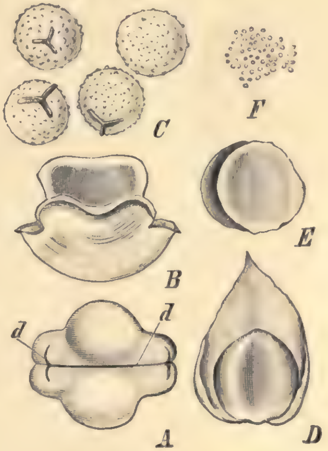


FIG. 425.—*Selaginella helvetica*. *A*, macrosporangium from above showing the line of dehiscence (*d*). *B*, opened, seen from the side; the four macrospores, *C*, have been ejected. *D*, microsporangium in the axil of its sporophyll. *E*, the same, opened. *F*, microspores. (× about 15.)

(cf. p. 50). At their ends a number of endogenous roots are produced, but the rhizophores are able, when the normal shoots are cut back, to continue their growth as shoots of ordinary construction. Even below the first leaves of the seedling plant short rhizophores are formed, from which the first roots arise endogenously. In many species of *Sclaginella* the epidermal assimilatory cells of the leaves possess, as in *Anthoceros*, only one large chloroplast ([121]).

As in *Lycopodium*, the cones or flowers are terminal. Each sporophyll subtends only one sporangium, which springs from the stem above the leaf-axil. The same spike bears both macrosporangia and microsporangia. Each macrosporangium (Fig. 425 *A-C*) contains only four macrospores, which are produced by the growth and division of a single spore-mother-cell; all the other mother-cells originally developed ultimately disappear. On account of the increasing size of the spores the spherical macrosporangia become nodular. Opening occurs along definite lines of dehiscence, the wall splitting into two valves, which curve back from a boat-shaped basal portion. The spores are ejected by the pressure of the contracting boat-shaped part and the valves. Numerous spores are formed in the flattened microsporangia. The mode of dehiscence is similar in these also, but the boat-shaped portion of the wall is smaller, the valves extending to the base.

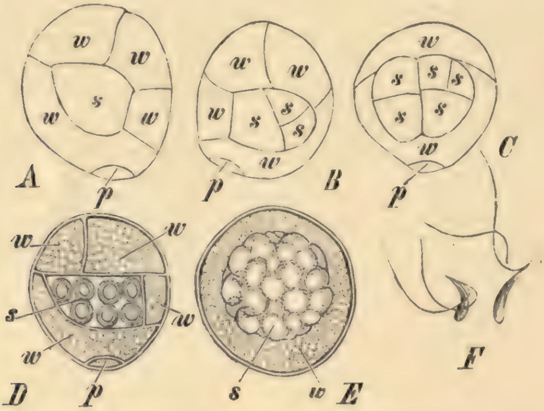


FIG. 426.—*A-E*, *Selaginella stolonifera*, successive stages in the germination of a microspore; *p*, prothallium-cell; *w*, wall-cells of antheridium; *s*, spermatogenous cells; *A*, *B*, *D*, lateral, *C*, dorsal view. In *E* the prothallium-cell is not visible, the disorganised wall-cells enclose the spermatozoid mother-cells; *F*, spermatozoids of *Selaginella cuspidata*. (After BELAJEFF. *A-E* × 640, *F* × 780.)

The microspores begin their development while still enclosed within the sporangium. The spore first divides into a small lenticular vegetative cell, which corresponds to the rhizoid cell of *Salvinia*, and into a large cell, which divides successively into eight sterile peripheral cells and two or four central spermatogenous cells (Fig. 426 *A*). By the further division of the central cells numerous spermatozoid mother-cells are formed (*B-D*). The peripheral cells then break down and give rise to a mucilaginous substance, in which is embedded the central mass of spermatozoid mother-cells (*E*). The small prothallium-cell, however, persists. Eventually the wall ruptures, and the mother-cells, thus liberated, set free the club-shaped biciliate spermatozoids (*F*). The reduction here exhibited in the formation of the male prothallium resembles that shown by the Hydropterideae.

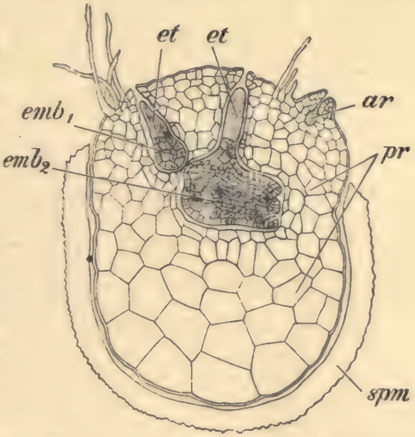


FIG. 427.—*Selaginella Martensii.* Female prothallium protruding from the apex of the ruptured macrospore; *spm*, wall of macrospore; *ar*, an unfertilised archegonium; *emb*$_1$, *emb*$_2$, two embryos, with suspensors *et*, sunk in the tissue of the prothallium. (After PFEFFER, modified, × 124.)

The macrospores in some species similarly begin their development within the sporangia. After the division of the nucleus—which lies in the peripheral cytoplasm at the apex—into daughter nuclei and their distribution in the apical cytoplasm, the formation of cell walls begins. In this way, progressing from apex to base, the spore becomes filled by a process of multicellular formation, with large prothallium-cells. At the same time, and proceeding in the same direction, there begins a further division of these cells into smaller cells. In some species the apical disc of tissue is formed first, and is separated by a thickened wall or diaphragm from the rest of the cavity of the spore; cell-formation occurs in this later. In the tissue at the apex, consisting of small cells, the rudiments of a few archegonia appear, often even before the formation of the prothallium has been completed. The archegonia are usually not formed until the spores have been discharged from the sporangium.

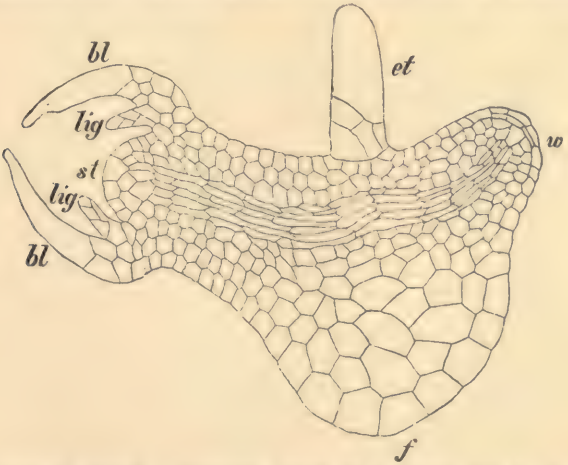


FIG. 428.—*Selaginella Martensii.* Longitudinal section of an embryo before its separation from the spore; *et*, suspensor; *w*, root; *f*, foot; *bl*. leaves; *lig*, ligules; *st*, apex of stem. (After PFEFFER, × 165.)

The wall of the spore eventually bursts at the apex, and the prothallium becomes partially protruded. The fertilisation of one or two archegonia, which then takes place, is followed directly by the segmentation of the fertilised egg-cells and the formation of the embryos (Fig. 427).

The embryogeny of *Selaginella* recalls that of *Lycopodium*. The egg-cell is divided by the formation of a transverse wall into two cells; the upper and larger cell increases considerably in size, and gives rise, by the division of its lower portion, to a suspensor (Fig. 428 *et*), while the lower cell, by repeated division, develops into an embryo, provided with two primary leaves and further segmented into stem, root, and foot (*bl*, *st*, *w*, *f*). The foot, in this instance, has a different position and origin than in *Lycopodium*. Each primary leaf has, even at this stage, a ligule (*lig*) formed as an outgrowth of the leaf-base.

The suspensor is perpendicular to the axis of the embryo; its function is to push the embryo into the tissue of the prothallium, with which the foot, the organ of absorption, is thus kept in close contact. The stem apex, with the first pair of leaves, eventually grows upwards, and the root also extends beyond the macrospore. As the foot still remains in the prothallium the young plant continues united to the spore, and presents the appearance of a phanerogamic seedling with the seed still attached (Fig. 424 *B*).

Order 3. Isoetaceae (122)

The isolated genus *Isoetes* must be regarded as a persistent branch of an ancient group of plants. It exhibits some affinities with the eusporangiate Ferns. The species of *Isoetes* are perennial plants, growing either on damp soil or submerged in water. The stem is short and tuberous, terminating below in a tuft of dichotomously branching roots, and above in a thick rosette of long, stiff, awl-shaped leaves (Fig. 429). The leaves are traversed longitudinally by four air-passages, and expand at the base into a broad sheath. On the inner side of the leaves, above their point of insertion, is an elongated pit, the fovea, containing a large sessile sporangium.

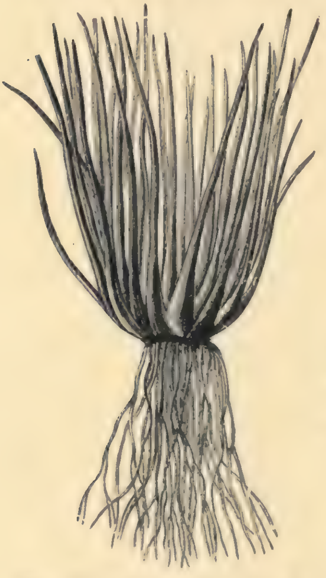


FIG. 429.—*Isoetes lacustris*. (½ nat. size.)

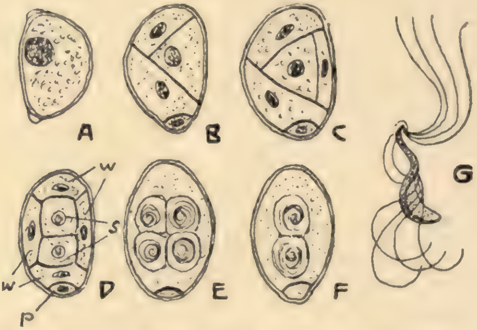


FIG. 430.—*A-F*, *Isoetes setacea* (× 640). *A*, microspore seen from the side. *B-D*, segmentation of the spore; *p*, prothallial cell; *w*, the four cells of the wall; *s*, spermatogenous cells. *E*, the four spermatozoid mother-cells are surrounded by the disorganised cells of the wall; surface view. *F*, the same in side view. *G*, *Isoetes Malinverniana*, spermatozoid. (× 780. After BELAJEFF.)

A ligule, in the form of a triangular membrane, is inserted above the fovea. *Isoetes* thus differs greatly in habit from the other genera, but resembles *Selaginella* in the development of a ligule.

The macrosporangia are situated on the outer leaves of the rosette; the microsporangia on the inner. Both are traversed by transverse plates of tissue or trabeculæ, and are in this way imperfectly divided into a series of chambers. The spores are set free by the decay of the sporangial walls.

The development of the sexual generation is accomplished in the same way as in *Selaginella*. The reduced male prothallium (Fig. 430) arises similarly within the spore, by the formation of a small, lenticular, vegetative cell, and a larger cell, the rudiment of a single antheridium. The larger cell divides further into four sterile peripheral cells, which completely enclose two central spermatogenous cells. From each of the latter arise, in turn, two spermatozoid mother-cells, four in all, each of which, when liberated by the rupture of the spore wall, gives rise to a single, spirally coiled, multiciliate spermatozoid. The female prothallium (Fig. 431) just as in *Selaginella*, also remains enclosed within the macrospore, and is incapable of independent growth. It shows similarly an approach to the Conifers, in that the nucleus first divides into numerous, parietal daughter-nuclei before the gradual formation of the cell walls, which takes place from the apex of the spore to the base. As a result of this process the whole spore becomes filled with a prothallium, at the apex of which the archegonia are developed. The embryo has no suspensor. In the structure of the embryo and of the spermatozoids *Isoetes* differs from the other Lycopodineae, and resembles in some respects the eusporangiate Ferns.

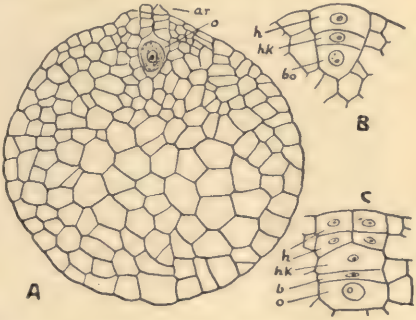


FIG. 431.—*Isoetes echinospora.* *A*, Female prothallium; *ar*, archegonium; *o*, egg-cell. *B*, *C*, development of the archegonium from a superficial cell; *h*, neck-cells; *hk*, neck canal-cell; *b*, ventral canal-cell; *o*, egg-cell. (After CAMPBELL, × 250.)

The Fossil Cryptogams (123)

The remains of cryptogamic plants of former geological periods afford no evidence as to the phylogenetic relations of the classes of Thallophyta and Bryophyta. Intermediate forms between Algae and Bryophyta and between the latter group and the Pteridophyta are, as yet, unknown. On the other hand Phytopalæontology has made us acquainted with interesting, long-extinct types of Pteridophytes, which serve to complete the classification of the existing Ferns, Horse-tails, and Club-mosses, and in part afford a transition from the Ferns to the Gymnosperms.

I. The great majority of **Thallophytes** are, on account of their delicate structure, not adapted to be preserved in the fossil condition. The absence of remains of many classes of Thallophytes is therefore no ground for concluding that they did not exist in earlier periods. Even in the Silurian rocks remains of Algae are found, though they do not permit of their relationship being determined. The remains of calcareous Algae belonging to the Siphonales are, owing to their good preservation, among the best known; of these, forms are known from the Tertiary strata back to the Silurian, while the Corallineae, which are calcareous Red Seaweeds, appear from the Upper Jurassic onwards. Among unicellular Algae the Diatomaceae, which have a silicified cell wall, are well preserved. The fossil forms frequently belong to existing genera, and occur from the Jurassic onwards, especially in the Cretaceous and Tertiary strata, often forming thick layers of Kieselguhr (diatomaceous earth). From Tertiary times onwards Characeae are abundant, and occasional remains are found as far back as the Muschelkalk. Most of the existing groups of Algae are only to be distinguished with certainty from Tertiary strata onwards.

Bacteria must have played their part in causing the decomposition of organic substances from very early times; they can be distinguished in vegetable remains from Carboniferous rocks. The Eumycetes and probably the Myxomycetes also, were present in Carboniferous times; Ascomycetes living on leaves and stems are found from the Carboniferous onwards in all strata. Remains of existing genera of Lichens appear in the Tertiary rocks.

II. **Bryophyta.**—Most of the examples of this group, which is rarely met with in the fossil condition, come from the Tertiary strata and resemble existing genera closely. Only isolated examples of Liverworts and Mosses occur in the older rocks (Jurassic, Upper Triassic).

III. The **Pteridophyta** extend back to Silurian times, but were most highly developed in the Carboniferous period, when they formed the main mass of the land vegetation. With the advent of Gymnosperms, and later of Angiosperms, their relative importance in this respect diminished.

1. The class of **Filicinae** was represented by forms belonging to both subclasses at the end of the Silurian period, and large numbers of species occur in the Carboniferous strata. The organisation of these ancient types is essentially similar to that of the existing forms. Most of the recent families were represented, some (*e.g.* Marattiaceae) more fully than at the present time. The Cycadofilices, fern-like plants with secondary thickening, which already bore seeds, appear to have given rise to the Phanerogams, or at least to the Cycadaceae. The other classes of Pteridophyta do not appear to have given origin to higher forms.

The Hydropterideae are known with certainty from the Tertiary rocks, but *Salvinia* and *Marsilia* can be traced back to the Chalk.

2. The class of the **Equisetinae** represented at present by the single genus *Equisetum*, which can be traced back to the Triassic period, was much better developed in Palæozoic times. The large order Calamarieae consisted of plants resembling the Horse-tails in general habit, but in some cases attaining the size of trees 30 metres high; the hollow stem bore whorls of branches at the nodes, was covered with a periderm, and underwent secondary thickening. The leaves (*Annularia*) stood in alternating whorls; their form was narrowly lanceolate and at their bases they united into a sheath. In the most ancient type, *Archaeocalamites*, they were dichotomously divided. The cones or flowers (*Calamostachys*) had in some the same structure as those of *Equisetum*; in most cases they were more complicated, whorls of scale-leaves alternating with the sporophylls. At least some of the Calamarieae were heterosporous.

3. The **Lycopodinae** were also abundantly represented in Palæozoic times, especially by the two great extinct orders, the Sigillarieae and the Lepidodendreae. The Sigillarieae, found from the Culm onwards, are most numerous in the Carboniferous period, and persist with one species in the Bunter Sandstone. They were stately trees, with but little branched, pillar-like stems, which grew in thick-

ness. They had long narrow leaves, which when they fell off left longitudinal rows of hexagonal leaf-scars on the surface of the stem. Long-stalked, cone-like flowers were borne on the stem; only one kind of spore was contained in the sporangia.

The Lepidodendreae extend from the Lower Devonian to the Rothliegende, but are also best developed in the Carboniferous period. They were tree-like plants with dichotomously branched stems which grew in thickness. The leaves, which attained a length of 15 cm., were spirally arranged and seated on rhombic leaf-cushions. The cone-like flowers (*Lepidostrobus*) were borne on the ends of branches or sprang from the stem itself; each sporophyll bore a single sporangium, which contained either macrospores or microspores.

Smaller Lycopodiaceae, the predecessors of the existing species of *Lycopodium*, were already present in the Carboniferous flora, while *Isoetes* is only known with certainty from the lower Cretaceous strata.

4. The small class of the **Sphenophyllinae**, which existed from the Devonian to the Permian and then died out, possesses special morphological interest since it occupies an intermediate position between Lycopodinae and Equisetinae. Possibly it is the least altered from the common ancestral form of these three groups. This especially holds for the most ancient type *Cheirostrobus*, which occurs in the Lower Carboniferous rocks. The cones of this genus had a very complicated structure, reminding one of the calamarian cone, while the anatomy exhibits an approximation to the type of *Lepidodendron*.

The species of *Sphenophyllum* were plants with elongated stems, bearing superposed whorls of obcuneate or more or less dichotomously divided leaves. The cones were large and terminal, resembling those of *Equisetum*; each sporophyll bore two or three homosporous sporangia. These plants have been regarded as aquatic, but the structure of the elongated thin stem, with a triangular mass of primary xylem and subsequent secondary thickening, rather suggests that they were climbing plants which grew on land.

PART II

SPECIAL BOTANY

SECTION II

PHANEROGAMIA

SECTION II

PHANEROGAMIA

The Transition from the Cryptogams to the Phanerogams.—The old names, Cryptogams and Phanerogams, are here retained partly on historical grounds and also because there are no better and equally short terms for the two great grades of the vegetable kingdom. The sharp distinction which formerly appeared to exist between the two groups has, however, as our knowledge has advanced, become less marked. The Phanerogams appear as a continuous development from heterosporous Vascular Cryptogams. The recognition of this is owing, in the first place, to the work of W. HOFMEISTER (1).

It has been seen (p. 422) that the existence of an alternation of generations is an essential character, common to both Bryophytes and Pteridophytes; the life history exhibits a regular alternation of a sexual with an asexual generation. While in the Bryophyta only the sexual generation attains an independent existence, in the Vascular Cryptogams this stage appears as the inconspicuous prothallium. The asexual generation, on the other hand, which in the Moss was represented by the sporogonium dependent throughout its life on the sexual plant, becomes physiologically independent in the Pteridophyta. In them it appears as the conspicuous plant, the Fern or Horsetail, and bears leaves, on some of which, the sporophylls, the sporangia develop. A shoot bearing a number of sporophylls, and frequently with other leaves forming an outer investment, is known as a FLOWER. Thus *Equisetum* (Fig. 420, p. 456) affords a good example of a flower of simple construction, in which the sporophylls are all alike.

The appearance of heterospory (p. 441) marks a most important advance; the sexual differentiation, which in homosporous forms did not appear until the sexual generation, is evident in the asexual plant. The latter produces male sporangia (the microsporangia) and female macrosporangia. The function of the sexual generation is limited to the production of the male or female sexual organs, and it undergoes still further reduction. In the germination of the microspores only a single, vegetative prothallium-cell is to be recognised, the remainder of the small prothallium representing one or more antheridia. The female prothallium, which in *Salvinia* still becomes green and emerges from the macrospore, in *Selaginella* and *Isoetes* has lost the power of independent nutrition. The prothallium begins its development while still within the macrosporangium of the parent plant, and the macrospore after being set free only opens in order to allow of the access of the spermatozoids to the archegonia.

Thus within the series of Vascular Cryptogams a reduction of the sexual generation can easily be traced; this reduction is carried further in those Phanerogams which stand nearest to the Cryptogams (²).

The MACROSPORE, which in the Phanerogams has for long been termed the EMBRYO-SAC, remains enclosed in the MACROSPORANGIUM or OVULE. The latter consists of the NUCELLUS, from the base of which (the CHALAZA) one or two INTEGUMENTS arise; these grow up as tubular investments of the nucellus and only leave a small passage, the MICROPYLE, leading to the tip of the latter. The ovule is attached to the MACRO-SPOROPHYLL or CARPEL by a stalk or FUNICULUS, which is often very short. The region to which one or more ovules are attached is called the PLACENTA. If the nucellus forms the direct continuation of the funiculus the ovule is termed straight or ATROPOUS. More frequently the funiculus is sharply curved just below the chalaza so that the ovule is bent back alongside its stalk (ANATROPOUS ovule). The line of junction of the funiculus with the outer integument is still recognisable in the ripe seed and is termed the RAPHE. Lastly the ovule itself may be curved, in which case it is spoken of as CAMPYLOTROPOUS. The three types are diagrammatically represented in Fig. 432 *A-C*.

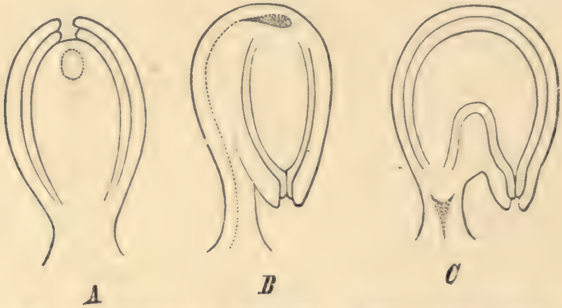


FIG. 432.—*A*, Atropous; *B*, anatropous; *C*, campylotropous ovules. (Diagrammatic and magnified.)

As a rule only one embryo-sac is contained in an ovule. In the same way as the four macrospores originate by the tetrad division in the macrosporangium of *Selaginella*, in the macrosporangium (ovule) of the Phanerogams there is usually a single embryo-sac mother-cell which divides into four daughter-cells; three of these do not develop further, while the fourth becomes the embryo-sac. The formation of the PROTHALLIUM or ENDOSPERM and of the ARCHEGONIA or EGG-CELLS differs in the several classes of Phanerogams. The fertilised ovum grows into the embryo while still enclosed within the macrospore and at the expense of the parent plant. When the embryo has reached a certain stage in its development, which is different and characteristic in different plants, its growth is arrested, and after the separation from the parent plant it undergoes a period of rest. It is still surrounded by the other portions of the macrosporangium, viz. the prothallium or endosperm, the nucellus (if this still persists), and the seed coat formed from the integuments. THE COMPLETE STRUCTURE DERIVED FROM THE OVULE IS TERMED A SEED, AND THE FURTHER DEVELOPMENT OF THE UNOPENED MACROSPORANGIUM TO FORM A SEED IS CHARACTERISTIC OF ALL PHANEROGAMS. As seed-plants or Spermaphyta the latter may be contrasted with the seedless Cryptogams.

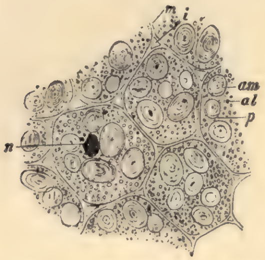


Fig. 433.—Part of section through one of the cotyledons of the Pea, showing cells with reserve material. *am*, Starch grains; *al*, aleurone grains; *p*, protoplasm; *n*, nucleus. (× 160.)

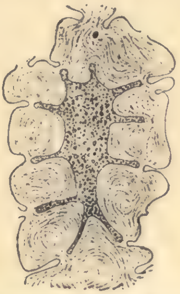


Fig. 434.—Cell from the endosperm of *Phytelephas macrocarpa*, with reserve cellulose. (× 225.)

The several parts of the ripe seed are thus the EMBRYO, the PROTHALLIUM or ENDOSPERM surrounding it, the remains of the NUCELLUS which is distinguished from the endosperm as PERISPERM, and the SEED-COAT. The cells of the endosperm and the perisperm when present are stored with reserve materials such as starch, proteid substances, or fatty oils (Figs. 433, 434); cellulose in the form of greatly thickened cell walls may also be a reserve substance. When the seed after a period of rest commences to germinate, these substances are utilised by the young plant until it becomes capable of independent nutrition. Since the nucellus is as a rule completely obliterated by the enlarging endosperm, few seeds possess a perisperm (Fig. 435). Frequently no endosperm is present in the seed, and the storage of reserve material takes place throughout the embryo (Fig. 436) or in its swollen seed-leaves or COTYLEDONS.

The SEED-COAT presents great variety in its appearance. It is always constructed to protect the tender parts within against drying or injury, and usually shows layers of cells with their walls thickened and lignified or suberised. On the outside of the seed-coat the scar of the funiculus can be distinguished, and is known as the HILUM; the MICROPYLE can also be seen, and in anatropous seeds the RAPHE marking the line of union between the funiculus and the integument, and extending from the hilum to the chalaza. In some cases an ARILLUS is developed from the funiculus; this is a succulent and usually brightly coloured structure, and stands in relation to the dispersal of the seed by animals. An outgrowth surrounding the micropyle is found in some seeds, especially those of the Euphorbiaceae, and is termed a CARUNCULA (Figs. 437, 438).

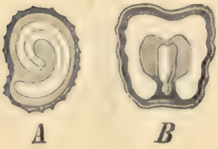


FIG. 435.—*A*, Seed of *Hyoscyamus niger*, showing the dicotyledonous embryo embedded in the endosperm; *B*, seed of *Elettaria Cardamomum*, enveloped by a thin aril; the white, mealy perisperm next to the seed-coat encloses an oleaginous endosperm (shaded), in which the monocotyledonous embryo lies embedded. (After BERG and SCHMIDT.)

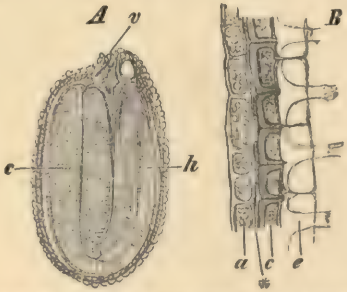


FIG. 436.—*Capsella bursa pastoris*. *A*, Longitudinal section of a ripe seed; *h*, hypocotyl; *c*, cotyledons; *v*, vascular bundle of the funicle (× 26); *B*, longitudinal section of the seed-coat after treatment with water; *e*, the swollen epidermis; *c*, brown, strongly thickened layer; *, compressed layer of cells; *a*, the single persisting layer of endosperm cells containing aleurone grains (× 250).

The effect of fertilisation is not only seen in the macrosporangia but extends to the macrosporophylls or carpels. The structures of very various form which are formed from the carpels (often together with the persistent calyx and the floral axis) are called FRUITS, and serve primarily to protect the developing seeds. The different forms of fruit will be frequently referred to in the special accounts of the classes and orders below.

The GERMINATION of the seed, *i.e.* the resumption of growth at the end of the resting period, must also be briefly considered. The chief condition of germination is the absorption of water. The embryo resumes its growth, which has for a time been arrested, ruptures the seed-coat and sends its root down into the soil. When it is in this way firmly fixed in position the cotyledons become free from the seed and expand in the light; when they remain within the seed-coat as in the Pea and Horse-chestnut, the plumule (*i.e.* the young shoot) is quickly developed at the expense of the reserve materials stored in the cotyledons (cf. Fig. 169; pp. 161 and 320).

An account of the male sexual generation of the Phanerogams must now be given for comparison with the above short sketch of the development of the female generation.

The MICROSPORES of the Spermaphyta are called POLLEN-GRAINS. They are formed in large numbers within the MICROSPORANGIA or POLLEN-SACS, which are borne singly or in numbers on the MICROSPOROPHYLLS or STAMENS. The part of the stamen which bears the pollen-sacs is usually clearly distinguishable and is called the ANTHER.

The development of the pollen-sac (Fig. 439) commences with divisions parallel to the surface taking place in cells of the hypodermal layer; this separates the cells of the primary archesporium from an outer layer of cells. The latter give rise to three layers of cells, the outermost of which is the fibrous layer, the innermost the tapetum, while the intervening layer is later crushed. The archesporium after undergoing a number of divisions forms the pollen-mother-cells, each of which divides as in Pteridophytes into four daughter-cells. These are the pollen-grains, and are spherical or ellipsoidal in shape and provided with a cell wall; an external cutinised layer (the EXINE), and an inner cellulose layer, rich in pectic substances (the INTINE), can be distinguished in the wall.

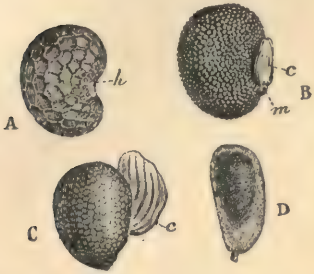


FIG. 437.—*A*, Seed of *Papaver Rhoeas*; *h*, the hilum; *B*, seed of *Corydalis ochroleuca*; *m*, micropyle; *c*, caruncula: *C*, seed of *Chelidonium majus*: *D*, seed of *Nymphaea alba* with its arillus. (After DUCHARTRE.)

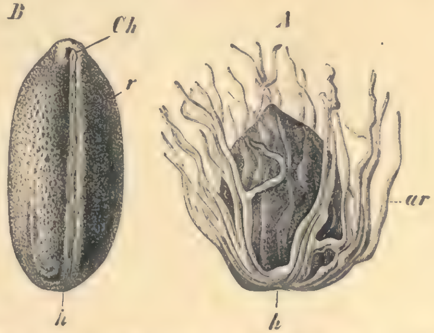


FIG. 438.—*A*, *Myristica fragrans*, seed from which the arillus (*ar*) is partly detached. *B*, *Myristica argentea*, seed after removal of the arillus; *ch*, chalaza; *r*, raphe: *h*, hilum. (After WARBURG. ⅔ nat. size.)

While the male sexual cells of all archegoniate plants are dependent on water for their conveyance to the female organs, the transport of the pollen-grains to the egg-cells is brought about in Seed-plants by means of the wind or by animals. However far the reduction of the male prothallium has proceeded—and even in the case of the heterosporous Pteridophyta only a single sterile cell was present,—two constituent parts are always distinguishable in the germinating pollen-grain; these are a VEGETATIVE CELL which grows out as the POLLEN-TUBE, and an ANTHERIDIAL MOTHER-CELL which ultimately gives rise to two GENERATIVE CELLS. The pollen-tube, the wall of which is continuous with the intine of the pollen-grain, ruptures the exine and penetrates, owing to its chemotropic irritability, into the tissue of the macrosporangium (cf. p. 286). The antheridial mother-cell passes into the pollen-tube and sooner or later gives rise to two generative cells which reach the embryo-sac and egg-cell by passing along the pollen-tube. The name Siphonogams has been applied to the seed-plants on account of the common character of the group afforded by the formation of a pollen-tube.

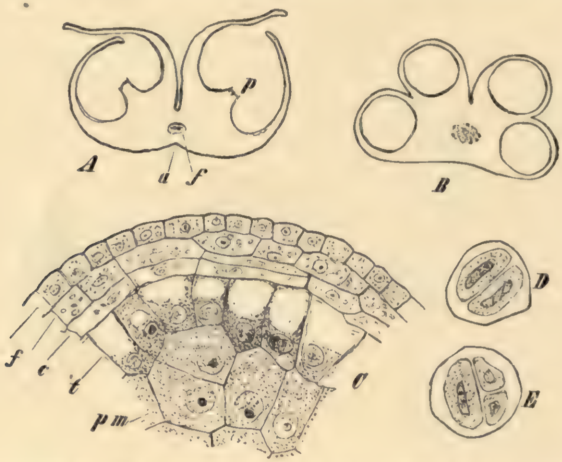
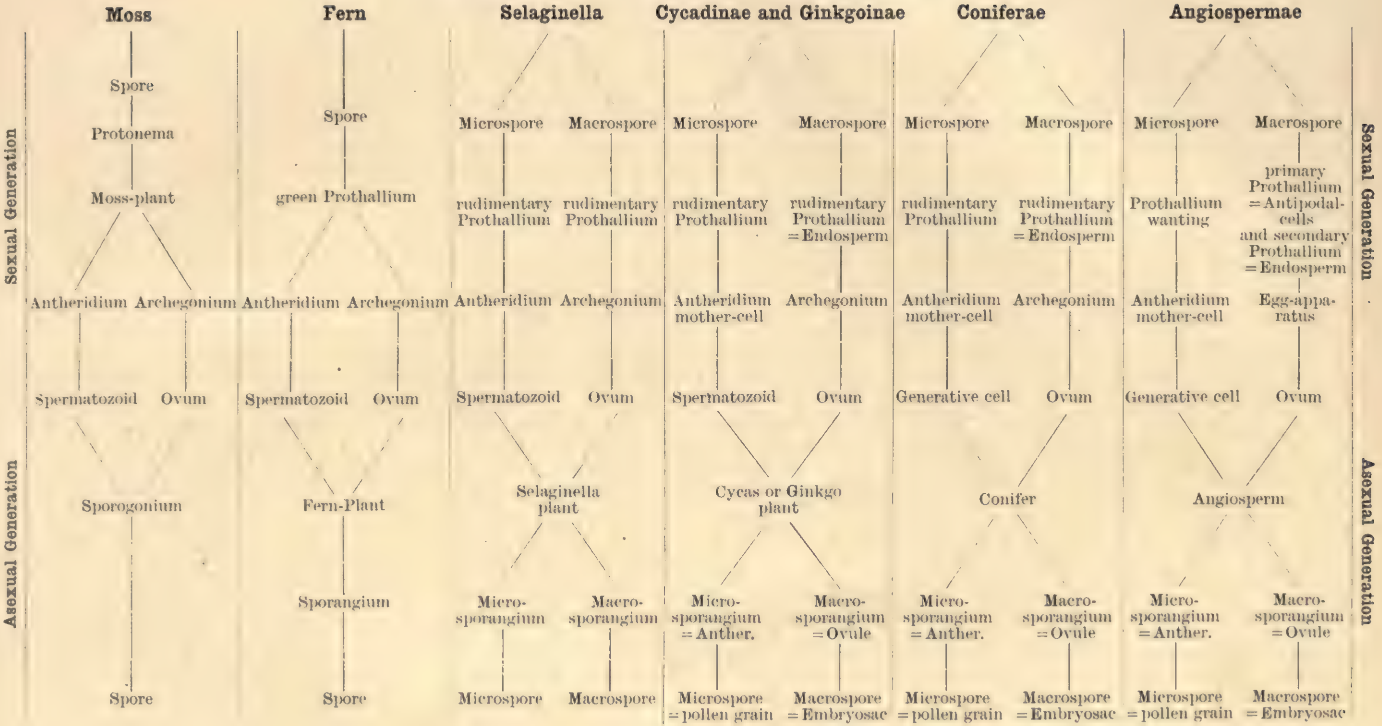


FIG. 439.—*Hemerocallis fulva.* *A*, Transverse section of an almost ripe anther, showing the loculi ruptured in cutting; *p*, partition wall between the loculi; *a*, groove in connective; *f*, vascular bundle (× 14); *B*, transverse section of young anther (× 28); *C*, part of transverse section of a pollen-sac; *pm*, pollen-mother-cells; *t*, tapetal layer, later undergoing dissolution; *c* intermediate parietal layer, becoming ultimately compressed and disorganised; *f*, parietal layer of eventually fibrous cells; *e* epidermis (× 240); *D* and *E*, pollen-mother-cells after division (× 240).

The results reached by the above survey may be summarised by saying that the Phanerogams continue the series of the Archegoniatae and agree with the latter in exhibiting an alternation of generations. While the asexual generation becomes more complex in form and more highly organised, there is a corresponding reduction of the sexual generation. The female sexual generation is enclosed throughout its whole development in the asexual plant, and only becomes separated from the latter in the seed, which further contains as the embryo the commencement of the succeeding asexual generation. The exhaustive investigations made of recent years into the phenomena of the

Scheme of Alternation of Generations


Sexual Generation
Asexual Generation
Moss
Spore
Protonema
Moss-plant
Antheridium
Archegonium
Spermatozoid
Ovum
Sporogonium
Spore
Fern
Spore
green Prothallium
Antheridium
Archegonium
Spermatozoid
Ovum
Fern-Plant
Sporangium
Spore
Selaginella
Microspore
Macrospore
rudimentary Prothallium
rudimentary Prothallium
Antheridium
Archegonium
Spermatozoid
Ovum
Selaginella plant
Micro-sporangium
Macro-sporangium
Microspore
Macrospore
Cycadinae and Ginkgoinae
Microspore
Macrospore
rudimentary Prothallium
rudimentary Prothallium = Endosperm
Antheridium mother-cell
Archegonium
Spermatozoid
Ovum
Cycas or Ginkgo plant
Micro-sporangium = Anther.
Macro-sporangium = Ovule
Microspore = pollen grain
Macrospore = Embryosac
Coniferae
Microspore
Macrospore
rudimentary Prothallium
rudimentary Prothallium = Endosperm
Antheridium mother-cell
Archegonium
Generative cell
Ovum
Conifer
Micro-sporangium = Anther.
Macro-sporangium = Ovule
Microspore = pollen grain
Macrospore = Embryosac
Angiospermae
Microspore
Macrospore
Prothallium wanting
primary Prothallium = Antipodal-cells and secondary Prothallium = Endosperm
Antheridium mother-cell
Egg-apparatus
Generative cell
Ovum
Angiosperm
Micro-sporangium = Anther.
Macro-sporangium = Ovule
Microspore = pollen grain
Macrospore = Embryosac
Sexual Generation
Asexual Generation

reduction division in the spore-mother-cells of archegoniates and Phanerogams have resulted in a confirmation of the limits of the two generations in the latter ([2a]). The number of chromosomes characteristic of any plant is diminished to one half during the divisions that lead to the origin of the sexual generation, and the full number of chromosomes is not again attained until fertilisation takes place. The asexual generation has always the double number, the sexual generation the single number of chromosomes. The constant progression of the former generation at the cost of the latter might be placed in relation with this difference between them; a strict demonstration of such a connection is, however, not possible.

The Spermaphyta are divided into two classes ([3]) which differ in their whole construction: (1) the Gymnosperms, with naked seeds; (2) the Angiosperms, with seeds enclosed in an ovary.

The names of these classes indicate the nature of one of the most important differences between them. THE CARPELS OF THE ANGIOSPERMS FORM A CLOSED CAVITY, THE OVARY, WITHIN WHICH THE OVULES DEVELOP. SUCH AN OVARY IS WANTING IN THE GYMNOSPERMS, THE OVULES OF WHICH ARE BORNE FREELY EXPOSED ON THE MACROSPOROPHYLLS OR CARPELS.

The Gymnosperms are the phylogenetically older group. Their construction is simpler and in the relations of their sexual generation they connect directly with the heterosporous Archegoniatae; they might indeed be perhaps best treated as belonging to this group.

The Angiosperms exhibit a much wider range in their morphological and anatomical structure. The course of their life-history differs considerably from that of the Gymnosperms, and without the intermediate links supplied by the latter group, the correspondence with the life-history of the Archegoniatae would not be so clearly recognisable.

These conclusions are confirmed by the evidence afforded by Palæobotany. Gymnosperms or forms resembling them are found along with what appear to be intermediate forms between the Gymnosperms and the Pteridophyta in the fossiliferous rocks of the Devonian, Carboniferous, and Permian formations. The Angiosperms are, on the other hand, first known from the Cretaceous formation.

Table of the Classes and the most Important Orders and Families of Phanerogams

Class I. Gymnospermae

1. *Cycadinae*: Fam. Cycadaceae.
2. *Ginkgoinae*: Fam. Ginkgoaceae.
3. *Coniferae*: Fam. Taxaceae, Pinaceae.
4. *Gnetinae*: Fam. Gnetaceae.

Class II. Angiospermae

Sub-Class A. Monocotylae

1. *Helobiae*: Fam. Alismaceae. Juncaginaceae. Potamogetonaceae. Naiadaceae. Hydrocharitaceae.
2. *Glumiflorae*: Fam. Cyperaceae. Gramineae.
3. *Spadiciflorae*: Fam. Typhaceae. Sparganiaceae. Pandanaceae. Palmae. Araceae. Lemnaceae.
4. *Enantioblastae*: Fam. Commelinaceae.
5. *Liliiflorae*: Fam. Juncaceae. Liliaceae. Amaryllidaceae. Iridaceae. Dioscoreaceae. Bromeliaceae.
6. *Scitamineae*: Fam. Musaceae. Zingiberaceae. Cannaceae. Marantaceae.
7. *Gynandrae*: Fam. Orchidaceae.

Sub-Class B. Dicotylae

(a) *Choripetalae*

1. *Piperinae*: Fam. Piperaceae. +
2. *Juglandiflorae*: Fam. Juglandaceae. Myricaceae.
3. *Saliciflorae*: Fam. Salicaceae.
4. *Querciflorae*: Fam. Betulaceae. Cupuliferae.
5. *Urticinae*: Fam. Ulmaceae. Moraceae. Cannabinaceae. Urticaceae.
6. *Centrospermae*: Fam. Polygonaceae. Chenopodiaceae. Caryophyllaceae.
7. *Polycarpicae*: Fam. Nymphaeaceae. Ceratophyllaceae. Ranunculaceae. Magnoliaceae. Anonaceae. Myristicaceae. Menispermaceae. Berberidaceae. Lauraceae.
8. *Rhoeadinae*: Fam. Papaveraceae. Cruciferae. Capparidaceae. Resedaceae.
9. *Insectivorae*: Fam. Sarraceniaceae. Nepenthaceae. Droseraceae. +
10. *Saxifraginae*: Fam. Crassulaceae. Saxifragaceae. Hamamelidaceae. +
11. *Rosiflorae*: Fam. Rosaceae.
12. *Leguminosae*: Fam. Mimosaceae. Caesalpiniaceae. Papilionaceae.
13. *Gruinales*: Fam. Geraniaceae. Oxalidaceae. Linaceae. Balsaminaceae. Erythroxylaceae. Zygophyllaceae. Rutaceae. Simarubaceae. Burseraceae. Polygalaceae.
14. *Tricoccae*: Fam. Euphorbiaceae. Callitrichaceae.
15. *Sapindinae*: Fam. Buxaceae. Anacardiaceae. Aquifoliaceae. Celastraceae. Aceraceae. Sapindaceae.
16. *Frangulinae*: Fam. Rhamnaceae. Vitaceae.
17. *Columniferae*: Fam. Tiliaceae. Sterculiaceae. Malvaceae.
18. *Cistiflorae*: Fam. Ternstroemiaceae. Guttiferae. Dipterocarpaceae. Cistaceae. Violaceae.
19. *Passiflorinae*: Fam. Passifloraceae. Caricaceae. Begoniaceae.
20. *Opuntinae*: Fam. Cactaceae.
21. *Thymelaeinae*: Fam. Thymelaeaceae. Elaeagnaceae.
22. *Myrtiflorae*: Fam. Lythraceae. Melastomaceae. Onagraceae. Halorrhagidaceae. Rhizophoraceae. Combretaceae. Myrtaceae. Punicaceae.
23. *Umbelliflorae*: Fam. Cornaceae. Araliaceae. Umbelliferae.
24. *Hysterophyta*: Fam. Aristolochiaceae. Santalaceae. Loranthaceae. Balanophoraceae. Rafflesiaceae.

(b) *Sympetalae*

(*α*) *Pentacyclicae.*

1. *Ericinae* : Fam. Ericaceae. Pirolaceae.
2. *Diospyrinae* : Fam. Sapotaceae. Ebenaceae. Styracaceae.
3. *Primulinae* : Fam. Primulaceae. Plumbaginaceae.

(*β*) *Tetracyclicae.*

4. *Contortae* : Fam. Oleaceae. Loganiaceae. Gentianaceae. Apocynaceae. Asclepiadaceae.
5. *Tubiflorae* : Fam. Convolvulaceae. Polemoniaceae. Hydrophyllaceae. Borraginaceae. Verbenaceae. Labiatae.
6. *Personatae* : Fam. Solanaceae. Scrophulariaceae. Orobanchaceae. Bignoniaceae. Gesneriaceae. Lentibulariaceae. Acanthaceae. Plantaginaceae.
7. *Rubiinae* : Fam. Rubiaceae. Caprifoliaceae. Valerianaceae.
8. *Campanulinae* : Fam. Campanulaceae. Lobeliaceae. Cucurbitaceae.
9. *Aggregatae* : Fam. Dipsacaceae. Compositae.

Class I. Gymnospermae (4)

Survey of the Development of the Sexual Generation

The flowers of the Gymnosperms are all unisexual. The macrosporophylls form the female, the microsporophylls the male flowers. The two sexes are found either on the same individual (MONŒCIOUS) or each plant bears either male or female flowers (DIŒCIOUS). Leaves forming an envelope around the group of sporophylls are found in only a few flowers of the Gymnospermae.

The MALE FLOWERS are shoots of limited length, the axis of which bears the closely crowded and usually spirally arranged sporophylls. The scales which invested the flower in the bud often persist at the base of the axis. The microsporangia are borne on the lower surface of the sporophylls, two or more being present on each. Their opening is determined as in the sporangia of the Pteridophyta by the peculiar construction of the outer layer of cells of the wall (exothecium). The pollen-grains are spherical, and are frequently provided with two sacs filled with air which increase their buoyancy and assist in their distribution by the wind (Fig. 440 *D*).

A prothallium consisting of a few cells is formed on the germination of the microspore. This lies within the large cell, which will later give rise to the pollen-tube, closely applied to the cell wall. The prothallium is composed of from 1 to 3 cells. The first-formed cells (Fig. 441 *A-C*, *v*) correspond to the vegetative cells of the prothallium. The spermatogenous cell (*sp*) which is cut off after these divides later into the mother-cell of the antheridium and a sterile sister-cell (*s*) adjoining the vegetative cells (Fig. 441 *B*, *D*). It is by the breaking down of this latter cell that the antheridial mother-cell becomes free to pass into the pollen-tube. On this taking place, or while the latter cell is still in its original position, it divides into two daughter-cells (*g*) ; these are the generative cells or the male sexual cells (Fig. 441 *E*). According to JUEL, *Cupressus* possesses a larger number of

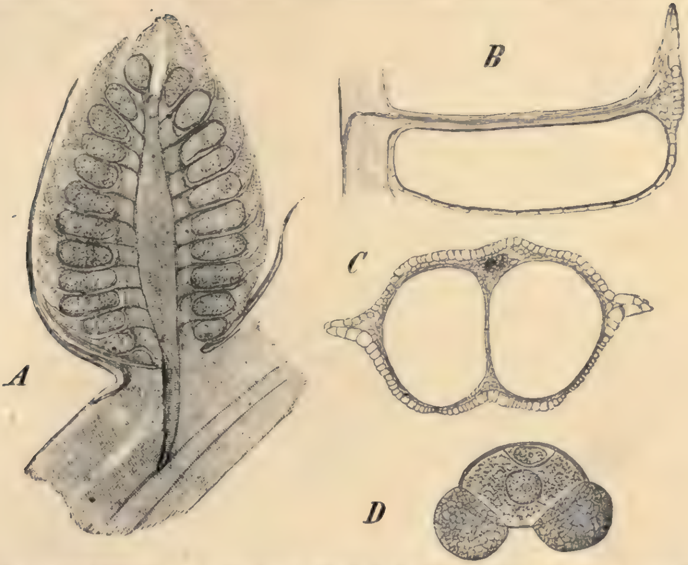


FIG. 440.—*Pinus montana.* *A*, Longitudinal section of a ripe male flower (× 10). *B*, Longitudinal section of a single stamen (× 20). *C*, Transverse section of a stamen (× 27). *D*, a ripe pollen-grain of *Pinus silvestris* (× 400).

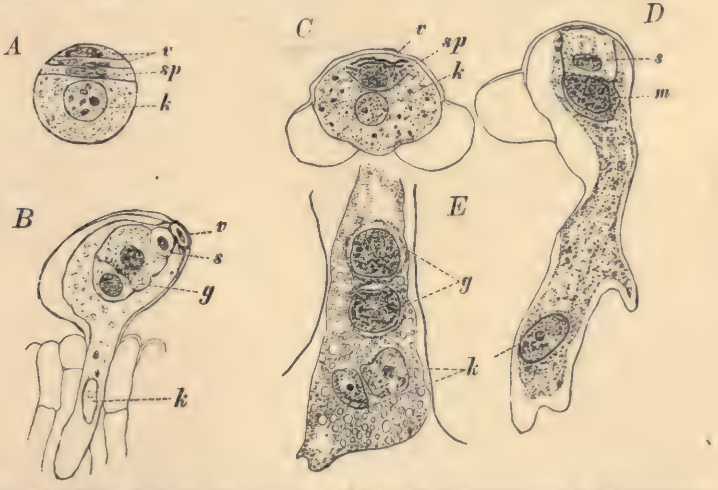


FIG. 441.—*A*-*E*, Pollen-grains of Gymnosperms and stages in the development of the pollen-tube *A*, Pollen-grain of *Ginkgo biloba* still enclosed in the sporangium (× 360). *B*, Pollen-grain of *Larix europaea* germinating on the tip of the nucellus (× 160). *C*-*E*, *Pinus Laricio* (after COULTER and CHAMBERLAIN ; *C*, *D* × 300, *E* × 250), *E*, tip of a pollen-tube which has reached the archegonium. *v*, Vegetative, prothallial cell ; *sp*. spermatogenous cell, which gives rise to the antheridial mother-cell (*m*) and its sterile sister-cell (*s*) ; *g*, the two generative cells derived by the division of the antheridial mother-cell ; *k*, nucleus of the pollen-tube, which in *E* cannot be distinguished with certainty from the nucleus of the disorganised cells.

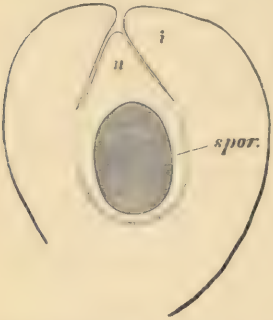


FIG. 442.—*Ceratozamia longifolia.* Longitudinal section through a young ovule, showing the nucellus (*n*), including a large group of sporogenous cells (*spor.*) and the integument (*i*). (After TREUB. × 33.)

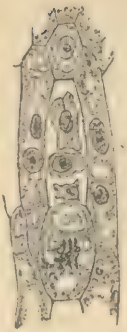


FIG. 443.—*Taxus baccata.* Longitudinal section through the sporogenous tissue, showing an embryo-sac mother-cell which has undergone the tetrad division; three of the facultative macrospores are degenerating, while the fourth is undergoing further development. (× 250.)

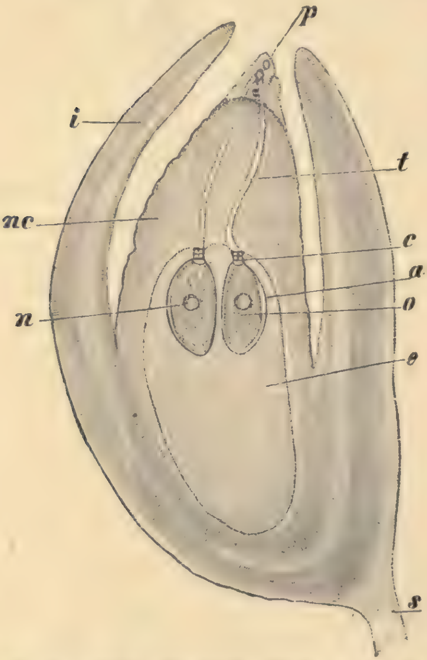


FIG. 444.—Median longitudinal section of an ovule of *Picea vulgaris.* *e*, Embryo-sac filled with the prothallium; *a*, archegonium showing ventral (*o*) and neck portion (*c*); *n*, nucleus of egg-cell; *nc*, nucellus; *p*, pollen-grains; *t*, pollen-tube; *t*, integument; *s*, seed-wing.

generative cells, while *Taxus* has only one. In the Cycadinae and Ginkgoinae the male cells appear as spermatozoids, while in the other Gymnosperms they are smooth cells not provided with a cell wall.

In many Gymnosperms the FEMALE FLOWERS or CONES resemble the male flowers in being composed of an axis bearing numerous, spirally arranged sporophylls. In other cases they differ from this type in various ways, which will be described in the special part below.

As a rule the macrosporophylls bear two macrosporangia; these consist of a nucellus and usually a single integument. The nucellus often becomes of large size by the numerous periclinal divisions which take place in the more superficial layers of cells. In the same way the sporogenous tissue, which originates immediately below the epidermis, becomes deeply placed by the separation of numerous layers of cells. Notwithstanding the considerable size of the sporogenous tissue only one, centrally placed macrospore-mother-cell is as a rule developed, all the other cells remaining sterile. The mother-cell undergoes a tetrad-division (Fig. 443), and of the four resulting cells only one develops into an embryo-sac (macrospore). This, as it increases in size, first crushes its sister-cells and later the whole sporogenous complex of cells. Meanwhile, by the repeated division of the nucleus and protoplasm, the macrospore becomes filled with the tissue of the prothallium (Fig. 444). The archegonia are formed at the apex of the prothallium; each consists of a large ovum and a short neck. As in the Pteridophytes a small ventral canal-cell is cut off from the egg-cell shortly before fertilisation. Fertilisation takes place by the entrance into the ovum of one of the generative cells, the development of which has already been followed; this enters from the pollen-tube, which penetrates between the cells of the archegonial neck. The nucleus of the fertilised ovum results from the fusion of the male and female sexual nuclei (Fig. 445) and the protoplasm is in part derived from the male cell. The development of the embryo from the fertilised ovum presents great differences in the several orders and even genera, and the following description applies to the species of *Pinus*.

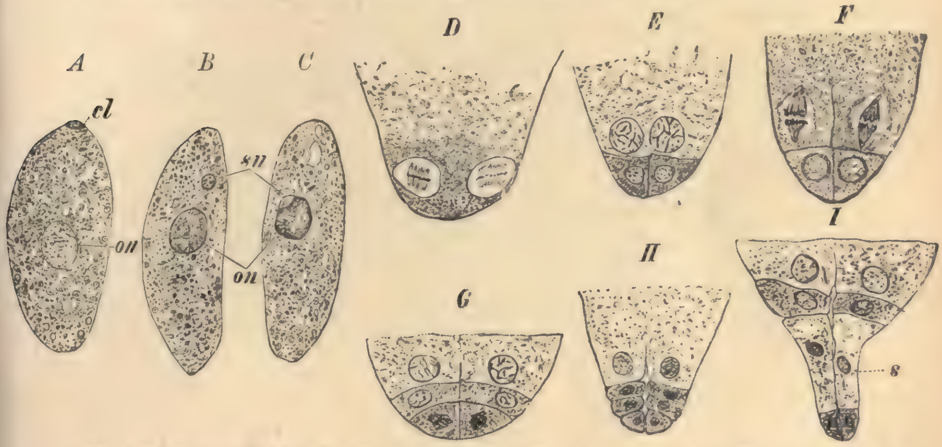


FIG. 445.—*Picea excelsa* (*A-C*, *F*). *Pinus laricio* (*D*, *E*, *G-I*). *A*, mature ovum with its nucleus (*on*) and the ventral-canal-cell (*cl*); *B*, the male nucleus (*sn*) within the ovum; *C*, fusion of the male and female nuclei; *D*, the four nuclei produced by division of the nucleus of the embryo have passed to the lower end of the ovum and are there in process of further division (only two of the nuclei are visible in the section); *E*, four of the eight nuclei are contained in independent cells, while the other four remain in the general cavity of the egg-cell; *F*, further division of the nuclei of the upper series; *G*, the cells of the lower tier have divided; *H*, four tiers of nuclei are present, those of the upper tier not being separated from the general cavity of the egg-cell; *I*, the elongation of the middle tier of four cells to form the suspensor (*s*) has commenced. (*A-C* × 55, *F* × 110, after MIYAKE; *D*, *E*, *G-I* × 104, after COULTER and CHAMBERLAIN.)

By two successive divisions of the nucleus four nuclei are formed which pass to the base of the egg-cell, where they arrange themselves in one plane and undergo a further division. Cell walls are formed between the eight nuclei of this eight-celled pro-embryo. The cells form two tiers, those of the upper tier being in open communication with the cavity of the ovum. The four upper cells then undergo another division, and this is followed by a similar division of the four lower cells. The PRO-EMBRYO thus consists of four tiers each containing four cells, the cells of the upper tier being continuous with the remaining portion of the ovum. In the further development of the three lower tiers the middle tier elongates to form the SUSPENSOR, pushing the terminal tier from which the embryo will arise into the tissue of the prothallium or endosperm; the cells of the latter are filled with nutritive reserve material.

In other genera a separation of the four rows of cells takes place, and each bears a young embryo. As a rule, however, only a single embryo continues its development in each macrospore although several archegonia may have been fertilised. The embryo consists of a main root or RADICLE directed towards the micropyle, an axis, the HYPOCOTYL, a whorl of from two to several COTYLEDONS and the PLUMULE or bud of the future shoot.

The asexual generation which shows less uniformity will be described under the separate orders.

Order 1. Cycadinae (5)

This includes the single Family, **Cycadaceae**. These are woody plants restricted to tropical and sub-tropical regions. The stem, which undergoes secondary growth in thickness, is as a rule unbranched and bears large, pinnate foliage leaves. These, which are of firm leathery texture and persist for a number of years, alternate with smaller scale-leaves and form a large terminal crown. The surface of the cylindrical or tuberous stem is clothed with the scale-leaves and the bases of the old foliage leaves. Mucilage ducts are present in all parts of the plant. The vascular bundles are collateral but their xylem consists of tracheides only.

The Cycadaceae are diœcious. Fig. 446 represents a female plant of *Cycas revoluta*, in which the growing point forms alternate zones of foliage leaves and macrosporophylls. When young the foliage leaves are rolled up circinately as in the Ferns. One of the sporophylls is represented in detail in Fig. 447. It shows the pinnate form of the foliage leaf but is densely covered with hairs, and chlorophyll is wanting. Towards the base two to eight macrosporangia are borne on the margins. It is evident that each female plant of *Cycas* which has reached the flowering condition exhibits a regular succession of flowering and vegetative periods. The flower represented by the group of sporophylls is always grown through by the further development of the apex which does not branch. The male plant of *Cycas* and the other Cycadaceae are morphologically more advanced in that they regularly produce lateral buds. Their sporophylls are borne in terminal cones often of great size, while the further growth of the plant is effected by a lateral bud which continues the direction of growth of the sympodial axis, displacing the cone to one side.

The cones consist of numerous sporophylls arranged spirally on the axis. The microsporophylls bear large numbers of microsporangia on the lower surface (Fig. 448). The macrosporophylls of the cone-bearing Cycadaceae are considerably modified as compared with *Cycas*, and each bears two marginal macrosporangia (Fig. 449); only in *Stangeria* are the macrosporangia situated on the lower surface.

The development of the sexual generation in the Cycadaceae differs in a number of respects from the general scheme for the Gymnosperms as given above. The differences indicate that the group is more closely connected with the Pteridophyta, and their nature will be evident from a description of *Zamia floridana*, which has been fully investigated by Webber.

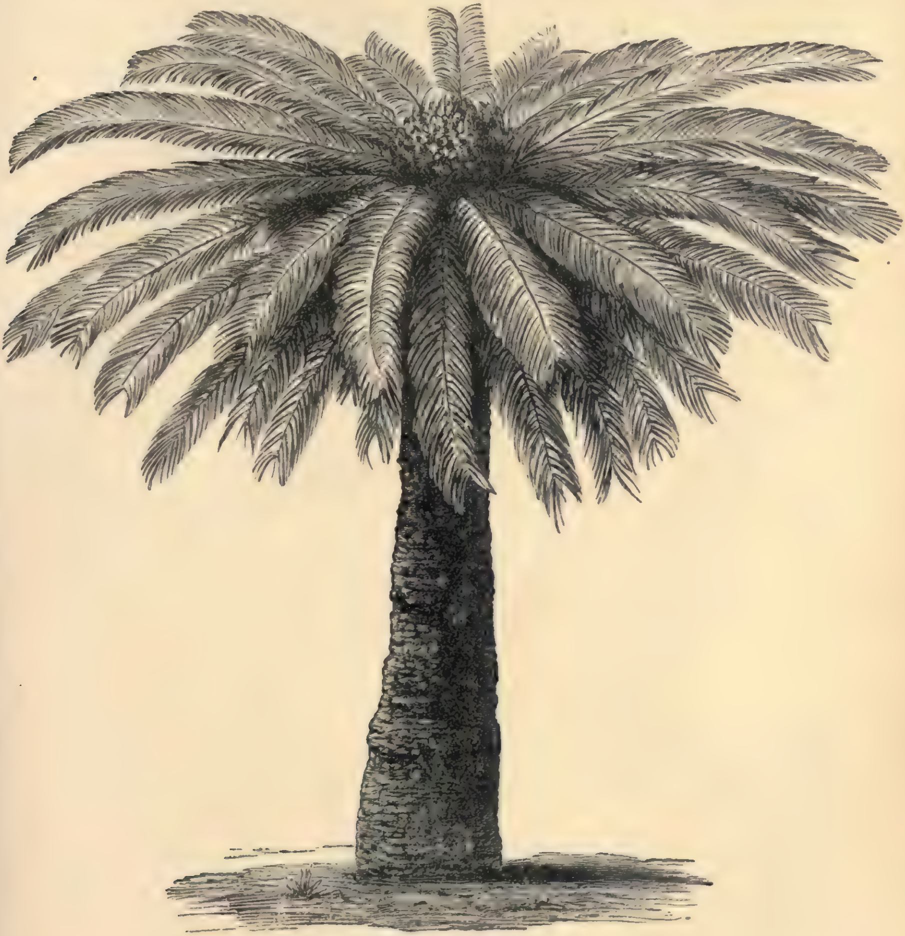


FIG. 446.—*Cycas revoluta*, female plant in flower. (From a photograph.)

The female cones of *Zamia* bear numerous sporophylls, the hexagonal shield-shaped terminal expansions of which fit closely together. Each sporophyll bears a pair of macrosporangia as is shown for *Ceratozamia* in Fig. 449. The macro-

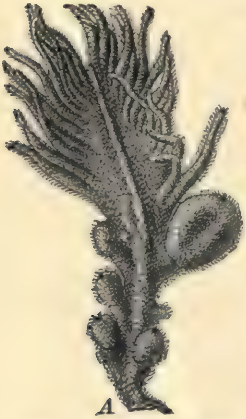


Fig. 447.—Carpel of *Cycas revoluta*. (After Sachs, reduced.)

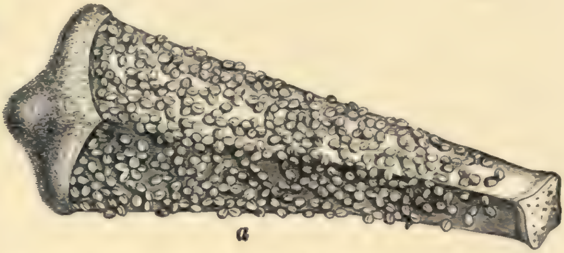


Fig. 448.—Stamen of *Cycas circinalis*, from below. (After Richard.)

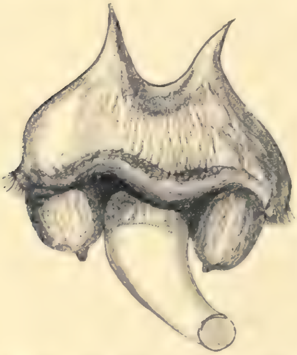


Fig. 449.—*Ceratozamia robusta*. Macrosporophyll with two macrosporangia. (After Goebel.)

sporangium consists of the nucellus and an integument. The micropyle forms an open canal above the tip of the nucellus. At the period during which the male cones are shedding their pollen, the macrosporophylls become slightly separated from one another so that the wind-borne pollen-grains can readily enter. A more or less extensive cavity (**pollen-chamber**) has by this time been formed at the apex of the nucellus, while the disintegrated cells, together perhaps with fluid excreted from the surrounding cells of the nucellus, form a sticky mass which fills the micropylar canal and forms a drop at its entrance. The pollen-grains reach this drop and, with the gradual drying up of the fluid, are drawn through the micropylar canal into the pollen-chamber. During the development of the pollen-tube and the formation of the motile spermatozoids, which have been found in all the Cycads yet investigated, the embryo-sac filled with the prothallial tissue is increasing in size within the nucellus. As it crushes the tissue of the upper portion of the nucellus it approaches the base of the pollen-chamber. At the apex of the embryo-sac are found the archegonia, usually four in number, and separated from one another by some layers of cells. Each archegonium has a neck, and ultimately cuts off a canal-cell. The archegonia are situated at the base of a depression in the prothallium, the archegonial chamber, which is about 1 mm. in depth and 2 mm. across. The pollen-tubes grow into this depression and liberate their spermatozoids together with a drop of watery fluid in which they swim. Since the bursting of the pollen-tubes is brought about by their contact with the projecting cells of the neck, the spermatozoids cannot easily lose their way to the egg-cell. They require, however, to narrow considerably in order to pass through the space between the neck cells. The nucleus of the fertilised ovum soon divides, and the daughter-nuclei continue to divide rapidly, until after the eighth division there are about 256 free nuclei within the cell. These are crowded towards the lower end of the pro-embryo, where cell-formation commences around them. The embryo is forced into the endosperm

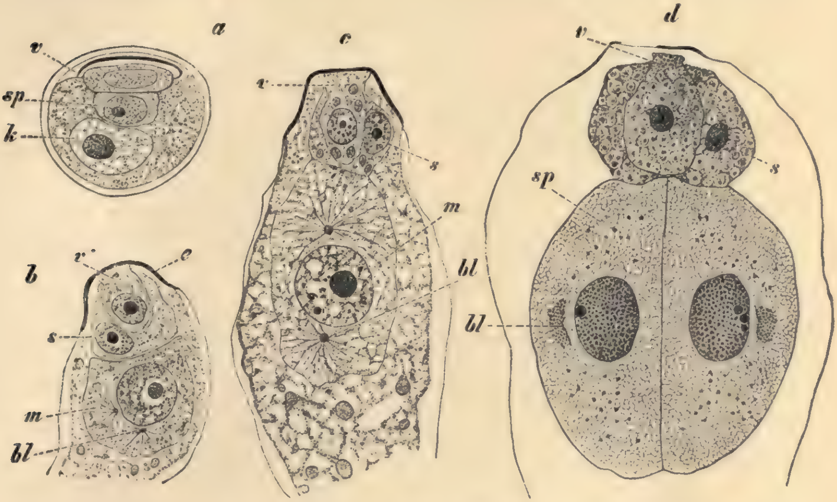


FIG. 450.—Formation of Spermatozoids in *Zamia floridana*. *a*, Mature pollen-grain (× 800); *v*, vegetative prothallial cell — the dark streak at its base indicates the position of another crushed cell; *k*, nucleus of the pollen-tube; *sp*, spermatogenous cell. *b*, *c*, *d*, stages in the development of the antheridium (*b*, *c* × 400; *d* × 200); *v*, persisting vegetative cell growing into the sterile sister-cell of the antheridium (*s*); *m*, mother-cell of the antheridium, *i.e.* mother-cell of the spermatozoids; *e*, exine. In the mother-cell the large blepharoplasts (*bl*) which form the cilia are visible; in *b* and *c* they are star-shaped, while in *d* they are composed of small granules, which will form the cilium-forming spiral band. Starch-grains are present in the pollen-tube, and in *c* they are appearing in the vegetative cell and the sister-cell, both of which in *d* are packed with starch. In *d* the two spermatozoids (*sp*) derived from the mother-cell are seen divided from one another by a wall. (After H. J. WEBBER.)

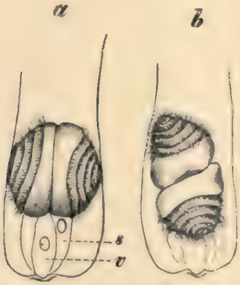


FIG. 451.—Upper end of the pollen-tube of *Zamia floridana*, showing the vegetative prothallial cell (*v*), the sterile sister-cell (*s*), and the two spermatozoids. *a*, Before movement of the spermatozoids has commenced; *b*, after the beginning of ciliary motion; the prothallial cell is broken down and the separation of the two spermatozoids is taking place. (× circa 75. After H. J. WEBBER.)

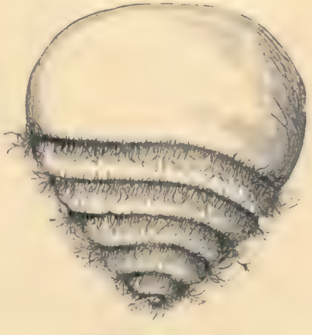


FIG. 452.—*Zamia floridana*. Mature, free-swimming spermatozoid. (× 150. After H. J. WEBBER.)

by the elongation of a suspensor. It ultimately possesses a pair of large cotyledons, a well-developed plumule between these and a relatively short hypocotyl (Figs. 450-453).

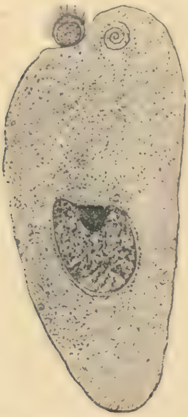


FIG. 453.—*Zamia floridana.* An ovum immediately after the fusion of the nucleus of a spermatozoid with the female nucleus has taken place. The ciliary band of the spermatozoid remains in the upper portion of the protoplasm of the ovum. A second spermatozoid has attempted to enter the ovum. (× 18, after H. J. WEBBER.)

Order 2. Ginkgoinae (6)

The single representative of the Family of the **Ginkgoaceae** which forms this order is *Ginkgo biloba.* This tree comes from Japan but is often seen in cultivation in Europe. The long-stalked leaves resemble those of an *Adiantum*, and are divided dichotomously into two or more lobes. The flowers are diœcious. The numerous stamens are situated on an elongated axis which bears no enveloping leaves. Microsporangia with an "*endothecium*" (cf. p. 503). Macrosporangia in pairs at the summit of short shoots; sporophylls reduced to a collar-like outgrowth around the base of the sporangium (Figs. 454, 455).

The development of the sexual generation and the fertilisation is very similar to what has been described for *Zamia*. The fertilised ovum

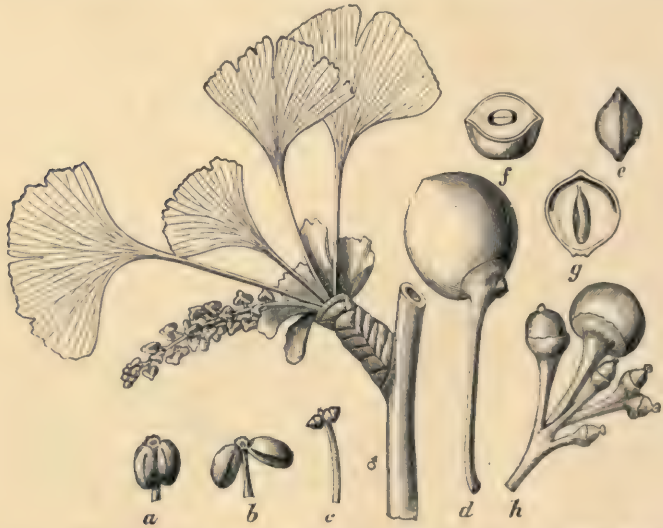


FIG. 454.—*Ginkgo biloba.* Male branch with flower; the leaves are not yet full grown. *a*, *b*, stamens; *c*, female flower; *d*, fruit; *e*, stone of same; *f*, stone in cross section; *g*, in longitudinal section showing the embryo; *h*, female flower with an exceptionally large number of ovules borne on separate stalks. (Male flower and *c*, nat. size; *d*, slightly reduced; the other figures magnified. After RICHARD; *a*-*d* after EICHLER.)

becomes filled with a continuous tissue and forms the embryo at the end farthest from the micropyle. This grows out and penetrates the endosperm, but there is no clear distinction into suspensor and embryo.

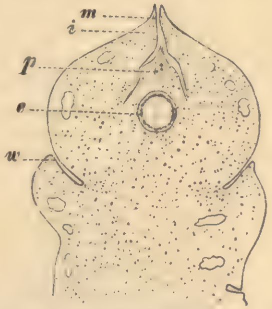


FIG. 455.—Longitudinal section of a young macrosporangium of *Ginkgo biloba*. *m*, micropyle; *i*, integument; *p*, pollen-chamber; *e*, embryo-sac; *w*, outgrowth of sporophyll. The possession of a well-developed pollen-chamber points to the relationship with the Cycadaceae. (× 35. After COULTER and CHAMBERLAIN.)

Order 3. Coniferae (7)

The Coniferae include conspicuous trees or shrubs with woody stems. The possession of small, undivided, firm leaves, flat or needle-shaped, and usually lasting for several seasons, is a common character of the plants of the order; they are thus for the most part evergreen. All Conifers are profusely branched, and a distinction into long and short shoots is usually evident. In many cases the direction and rapidity of growth of the main axis differs from that of the lateral branches. This is especially seen in young individuals; old trees are often more irregular in outline.

The absence of vessels from the xylem of young plants and from the secondary wood is an anatomical characteristic (cf. p. 134). Their place is taken by large tracheides with peculiar bordered pits on the radial walls; these form a very uniform wood. The majority of the Coniferae have resin abundantly present in all the parts of the plant.

The Coniferae in contrast to the Cycadinae are mostly inhabitants of temperate regions, and are among the trees which approach nearest to the polar regions. Within the tropics they are mostly confined to mountains.

The Coniferae are divided into two families on account of differences in the floral structure.

The *Taxaceae* have female flowers with one or few macrosporangia; the latter are usually provided with an arillus. The flowers are usually not definite cones. Mostly diœcious.

The *Pinaceae* on the other hand have a number of ovules in each female flower, the latter being a cone with numerous sporophylls borne on an axis. Arillus not present, usually monoecious.

Family **Taxaceae**.—The plants belonging to this family are grouped in a number of small genera distributed in the southern hemisphere. The most important genus is *Podocarpus*, the numerous species of which are widely distributed in temperate East Asia and in Australia and New Zealand, and also occur as stately trees on the mountains of the Asiatic tropics. The female flowers are small shoots, the sporophylls of which are swollen and succulent: one or two of them bear at the summit a single anatropous ovule surrounded by a fleshy arillus. The male flowers, which are borne on the same or on distinct individuals, are small cones consisting of numerous sporophylls attached to a short erect axis. Each sporophyll bears two microsporangia on the lower surface; the microspores are provided with distended wings.

Taxus baccata is the only European representative of the family. The Yew, which is now for the most part artificially introduced, had formerly a wide distribution as an evergreen undergrowth in our native woods (Figs. 456, 457). Isolated examples of large size occur in North and Central Germany, and it occurs as a more important constituent of the vegetation in Switzerland, *e.g.* on the steep slopes at Uetli. The Yew tree attains a height of 10 m. All the branches are shoots of unlimited growth. The leaves stand on all sides of the ascending main shoots but in two rows on the horizontally expanded lateral branches. They are narrow, flat leaves and persist for several years. The tree is diœcious; the flowers are situated on the lower surface of the twigs and arise in the axils of the leaves of the preceding year. The male flowers are invested at the base by a number of scale leaves and contain some 10 peltate stamens, each of which bears 5-9 pollen-sacs. The mode of opening of the sporangia is peculiar. The outer wall

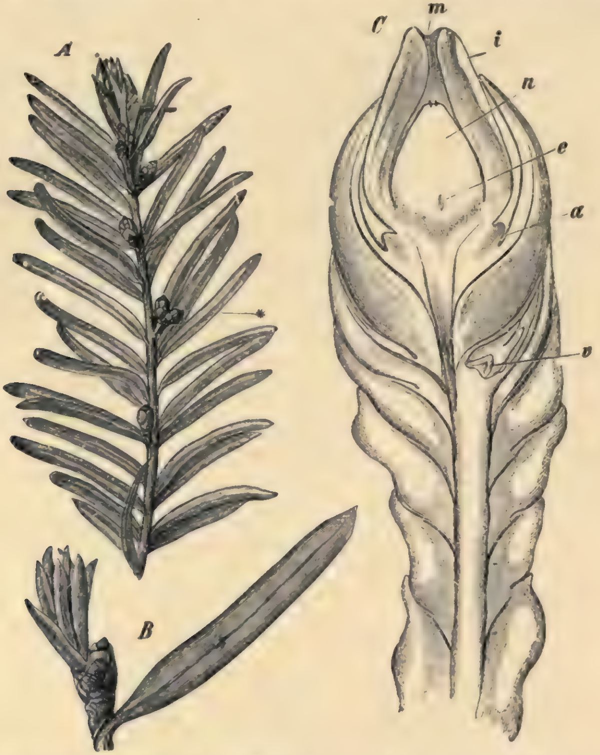


FIG. 456.—*Taxus baccata.* *A*, branch with female flowers: *, two ovules on the same shoot (nat. size); *B*, leaf with axillary, fertile shoot (× 2); *C*, median longitudinal section of a primary and secondary shoot; *v*, vegetative cone of the primary shoot; *a*, rudiment of the aril; *e*, rudiment of the embryo-sac; *n*, nucellus; *i*, integument; *m*, micropyle (× 48). *POISONOUS.*

splits at the base and along the side of each pollen-sac, so that the whole stamen resembles an umbrella turned inside out; the pollen remains for a time in the pocket-like depressions, from which it is removed by the wind. The female flower usually develops singly as a secondary, axillary shoot of the uppermost scale leaf of a primary shoot; the apex of the latter is displaced to the side and does not develop further. Each flower consists of a single, atropous ovule with one integument. The drop of fluid excreted from the micropyle of many Gymnosperms is especially well shown by the Yew. As the seed develops, a fleshy arillus springs from its base and surrounds the mature seed like a bright red cup. The foliage and seed are poisonous, but the aril, which induces birds to distribute the seed, is harmless.

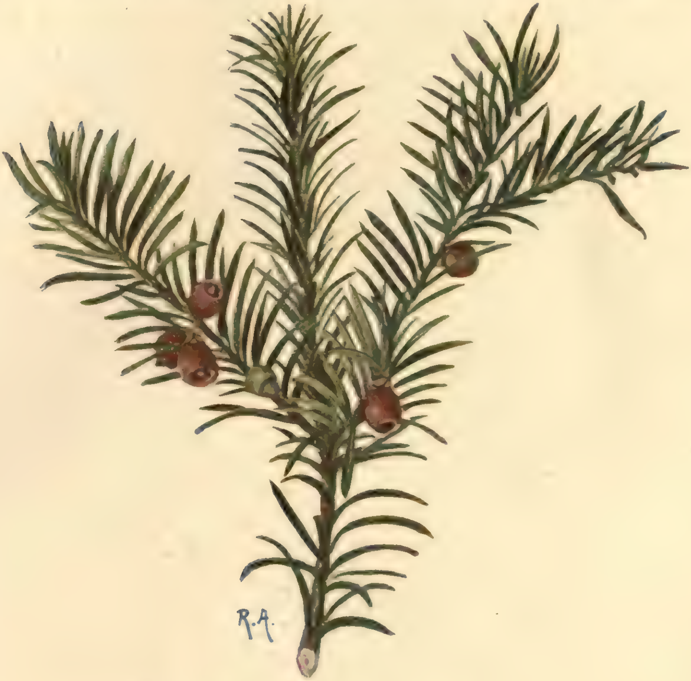


FIG. 457.—*Taxus baccata.* (½ nat. size.) *POISONOUS.*

Family **Pinaceae.**—This family includes the most important Coniferae, and on grounds of differences in leaf arrangement and in the position of the ovules is divided into two sub-families. The forms with the leaves opposite or in whorls are included in the *Cupressineae*; they also have the ovules erect. *Cupressus*, *Thuja*, *Juniperus*, and *Taxodium* are representative genera; the habit of *Taxodium* is peculiar. All the forms with alternate leaves are included in the *Abietineae*, and, almost without exception, they also possess inverted ovules. The genera *Araucaria* and *Agathis*—*Sequoia* and *Sciadopitys*—*Abies*, *Picea*, *Larix*, and *Pinus*, may be distributed in three distinct groups which may be named Araucarieae, Sequoieae, and Abietineae, in the narrow sense.

Sub-family **Cupressineae**.—Some of the Cupressineae have needle-shaped leaves in whorls (Juniper, Fig. 458), others have decussately arranged, scale-like leaves (*Thuja*, *Juniperus sabina*, Fig. 459). The former type is to be regarded as the more primitive, for the seedlings of *Thuja* have needle-shaped leaves, and individual branches of scale-leaved forms of *Juniperus* revert to the needle-shaped leaves in whorls of three. The short shoots of *Taxodium* have two ranks of leaves and are shed as a whole.

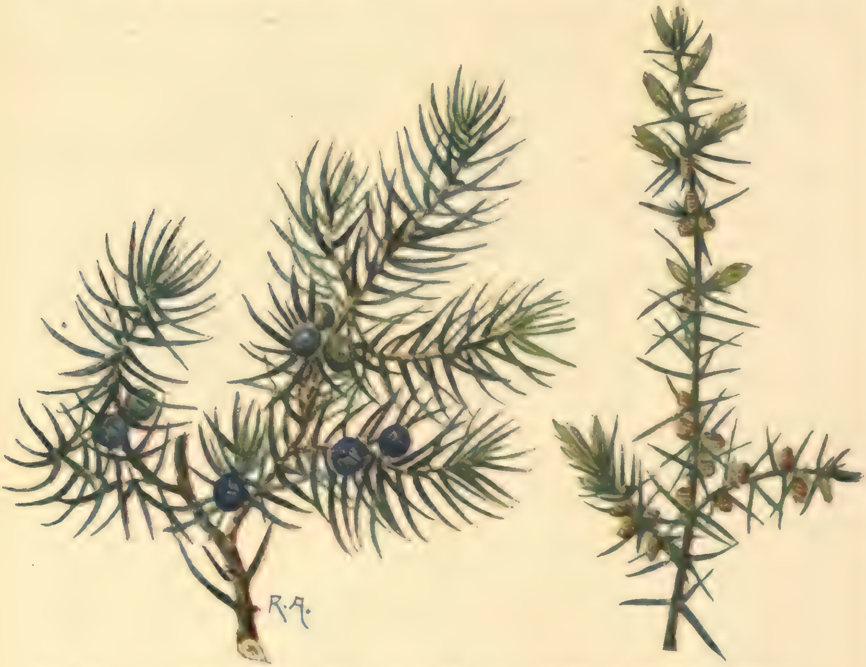


FIG. 458.—*Juniperus communis.* Twigs bearing fruits and male flowers. (⅔ nat. size.) *OFFICIAL.*

The Cupressinae, with the exception of *Juniperus*, are monœcious. The male flowers of *Juniperus communis* stand in the leaf axils. At their base are a number of small scale-leaves (Fig. 460 a, *a*), above which come several whorls of peltate sporophylls (*c*) bearing 2-4 microsporangia (*d*) on the lower surface. The sporangia open by a vertical slit parallel to the long axis of the sporophyll. The female flowers occupy a corresponding position. The scale leaves at the base (Fig. 460 b) are succeeded by a whorl of carpels (c, *b*), each of which bears a single upright ovule in a median position (*c*). After fertilisation a succulent parenchymatous growth mainly of the basal portions of the sporophylls raises the seeds and presses them together, without, however, obliterating the central space altogether. The three carpels become completely coherent above the seeds, but the place of union is still indicated by the scar at the apex of the ripe fruit; the tip of each carpel is a little back from the corresponding angle of the suture. The fruit takes two years to ripen. The succulence of the carpels gives the fruit the appearance of a berry.

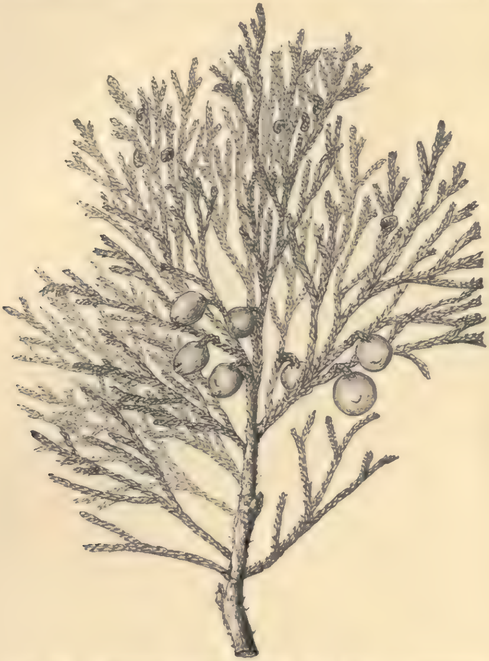


FIG. 459.—*Juniperus Sabina*: branch with fruit. *POISONOUS.*

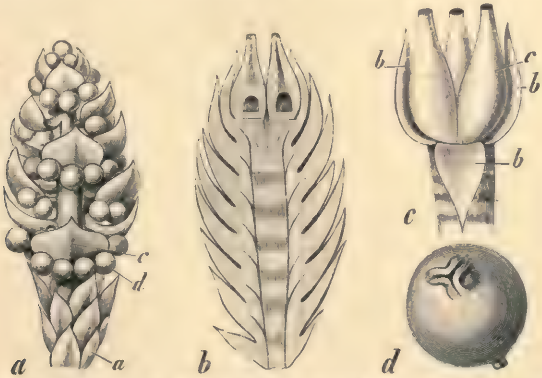


FIG. 460.—*Juniperus communis.* *a*, Male flower; *b*, fertile shoot with female flower; *c*, female flower with one scale bent out of place; *d*, fruit. *OFFICIAL.* (After BERG and SCHMIDT, all magnified.)

Juniperus is the only genus of the Cupressineae with such fruits ; the others, such as *Cupressus*, *Thuja*, *Taxodium*, have cones.

Juniperus communis, Juniper, is a shrub or small tree distributed over the northern hemisphere. *J. Sabina* a prostrate shrub of the Alps and other mountains of central and southern Europe. The Cypress (*Cupressus sempervirens*) in the Mediterranean region. *Taxodium distichum* is a deciduous tree, forming extended swampy woods on the north coast of the Gulf of Mexico from Florida to Galveston. *T. mexicanum* is evergreen and is widely distributed on the highlands of Mexico ; very large specimens occur such as the giant tree of Tule, which at a height of 40 m. was 30 m. in circumference, and was estimated by von Humboldt to be 4000 years old.

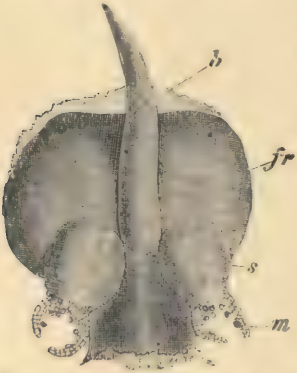


Fig. 461.—*Pinus silvestris.* Ovuliferous scale (*fr*) bearing two ovules *s* and the keel *c.* The bract scale *b* is visible behind. The free margin of the integument of the ovule forms two prolongations (*m*). (× 7.)

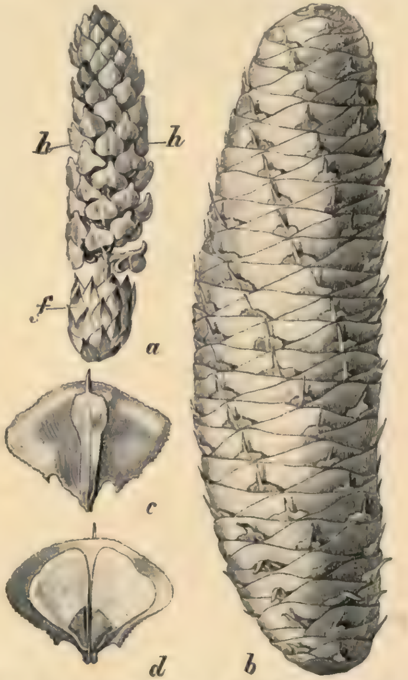


Fig. 462.—*Abies pectinata.* *a*, Male flower ; *f*, scale leaves ; *h*, sporophylls. *b*, Cone. *c*, Carpel, viewed from below (dorsal surface), showing the fertile and cover-scale ; *d*, the same viewed from above (ventral surface). (After Berg and Schmidt ; *a*, *c*, *d*, nat. size ; *b*, reduced.)

Sub-family **Abietineae**.—The floral structure of the Abietineae may be described in the first place. The male flowers (cf. Fig. 440, p. 481) consist of an axis bearing scale leaves at the base, and, above this, numerous stamens ; the pollen-sacs (microsporangia) are situated on the lower surface of the stamen. In the Abietineae in the narrower sense there are two pollen-sacs, but in *Agathis* and *Araucaria* there are 5-15. The projecting tip of the sporophyll varies in size and appearance, but is as a rule triangular. The microspores are usually winged. The female flowers are always cones, consisting of an axis bearing the closely approximated scales, which protect the ovules ; the scales later become lignified. In *Agathis* and *Araucaria* each scale bears a single anatropous ovule at its base. (The cone-bearing *Cupressineae* have an outgrowth of the scale on which the ovules are seated ; the outgrowth is not sharply marked off from the scale.) The condition of affairs in *Sequoia* and *Sciadopitys* is similar, but the outgrowth is more definitely defined ; each scale bears 4-9 anatropous ovules. In the Abietineae proper the limits of the two scales are still more marked. The two anatropous ovules are borne on an inner scale, which, at its base, is continuous with the scale of the cone. THE OUTER SCALE IS CALLED THE BRACT SCALE, THE INNER, THE OVULIFEROUS SCALE (Figs. 461, 462). The ovuliferous scale is the more strongly developed and it is the part that becomes lignified and affords protection to the ovules. Even at the period of flowering the bract scale is usually concealed by the ovuliferous scale and only to be detected on close inspection. In other forms, however (*e.g. Abies bracteata*, *A. pectinata*, Fig. 462 *b*, *Pseudotsuga Douglasii*, etc.), the bract scales even in the older cone project prominently between the ovuliferous scales.

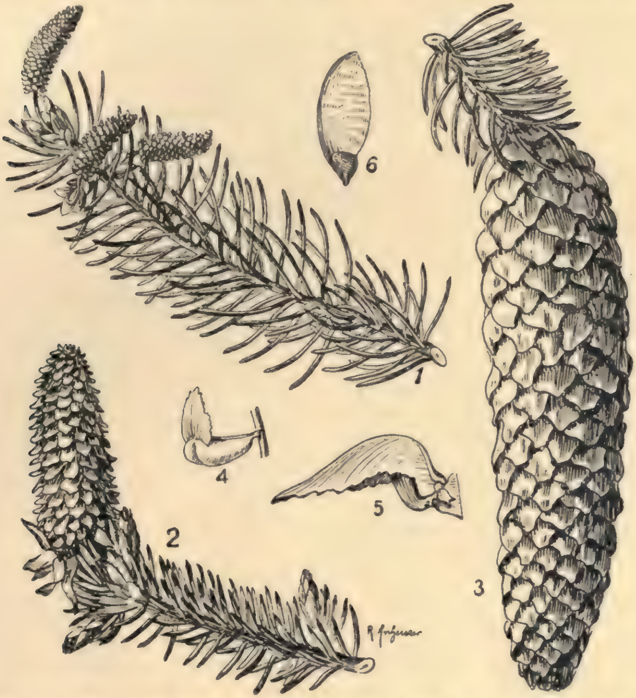


FIG. 463.—*Picea excelsa* (½ nat. size). *1*, Twig with male flowers. *2*, Terminal female flower. *3*, Pendulous cone. *4*, Microsporophyll. *5*, Macrosporophyll; the bract-scale is covered by the large, bent-back, ovuliferous scale; an ovule is visible at the base of the ovuliferous scale. *6*, Ripe seed with the wing formed by a detached portion of the ovuliferous scale. (× 4-6.)

The view here followed, that the ovuliferous scale is a placental outgrowth of the bract scale bearing the macrosporangia, and that its increase in size can be traced in the series of the Araucarieae and Abietineae, is that supported by SACHS, EICHLER, and GOEBEL. Attention must be drawn, however, to an alternative view supported by STRASBURGER and CELAKOVSKY among others. According to this the ovuliferous scale corresponds to the coherent bracteoles of an axillary shoot borne in the axil of the bract scale. The cone itself would thus not correspond to a single flower bearing a number of sporophylls, but to a system of shoots, *i.e.* it would be an inflorescence.

Most important Genera and Species.—*Agathis* (*Dammara*) is distributed in the Malayan Archipelago and extends to New Zealand; *A. australis* and *A. Dammara* yield Kauri Copal but no Dammar Resin; *Araucaria brasiliana* and *A. imbricata* are stately, S. American, forest trees; *A. excelsa*, *A. Cookii*, and other species with very limited distribution are extensively cultivated as ornamental trees. The genus *Sequoia* includes the most gigantic trees known; specimens of *S. gigantea* from the Californian Sierra Nevada attain a height of 100 m. and a diameter of 12 m.

European Forest Trees.—*Picea excelsa*, the Fir (Fig. 463), is a fine tree of pyramidal shape; it has no short shoots, and the long shoots bear on all sides pointed, quadrangular, needle-shaped leaves, which on horizontal or pendulous branches stand more or less erect. Male flowers as a rule on shoots of the previous year; on flowering they become twisted into an erect position. The two pollen-sacs open by a longitudinal slit. Female flowers terminal on the shoots of the previous year usually near the summit of the tree. They stand erect at the time of flowering. The ripe cones are pendulous and, after setting the seeds free from between the scales, fall in pieces. The development of the seeds is completed in one year. The male and female flowers occur on the same individual. *Picea orientalis* from Asia Minor, and *Picea alba* from N. America are frequently cultivated.

The Silver Fir (*Abies pectinata*, Fig. 462) is a native of the mountains of the middle and south of Europe. It bears only long shoots. The flat, needle-like leaves, marked below by two white lines and emarginate at the tip, are borne on all sides of the axis, but are twisted into a horizontal position on the branches illuminated from above. The male flowers stand in the leaf-axils on the under side or on the flanks of the shoot, and grow downwards so that the pollen-sacs are directed upwards. The wall of the sporangium opens by an obliquely longitudinal split, which gapes widely and allows the winged microspores to escape. The female flowers arise from the upper side of a branch and are directed vertically upwards. The bract-scales are longer than the broad, ovuliferous scales. The fertilised cones retain the upright position, and when ripe the scales separate from the axis and so set the seeds free from the plant. The development of the seeds takes a year. *Abies Nordmanniana* from the Caucasus, *A. pinsapo* from Spain, *A. concolor*, *A. balsamea*, and *A. nobilis* from N. America are in cultivation.

Larix europaea, the Larch, is one of the few deciduous Conifers and replaces its foliage annually. There is a differentiation into long and short shoots. The former bear the narrow linear leaves on all sides and continue the branching of the pyramidal tree the lower branches of which often droop downwards. The short shoots arise in the axils of the leaves of the long shoots of the preceding year, and bear a rosette of 30-40 leaves which are somewhat shorter but resemble those of the long shoots. The flowers occur in a position corresponding to that of the short shoots. The male flowers are bent downwards when fully developed, and the opening of the upwardly directed pollen-sacs occurs as in *Abies*. The erect female cones produce seed in the same year.

The most advanced differentiation of the vegetative organs is found in the genus *Pinus*; *P. silvestris*, the Scotch Fir, will serve as an example (Fig. 464). Young seedlings in the first or second year have long shoots bearing needle-shaped leaves. On older plants this type of foliage is lost; the needles are replaced by colourless, membranous scale leaves in the axils of which stand the short shoots. These have 2—in other species 3 or 5—needle-shaped foliage leaves. The latter are about 5 cm. in length, their flat surfaces are turned to face one another and the

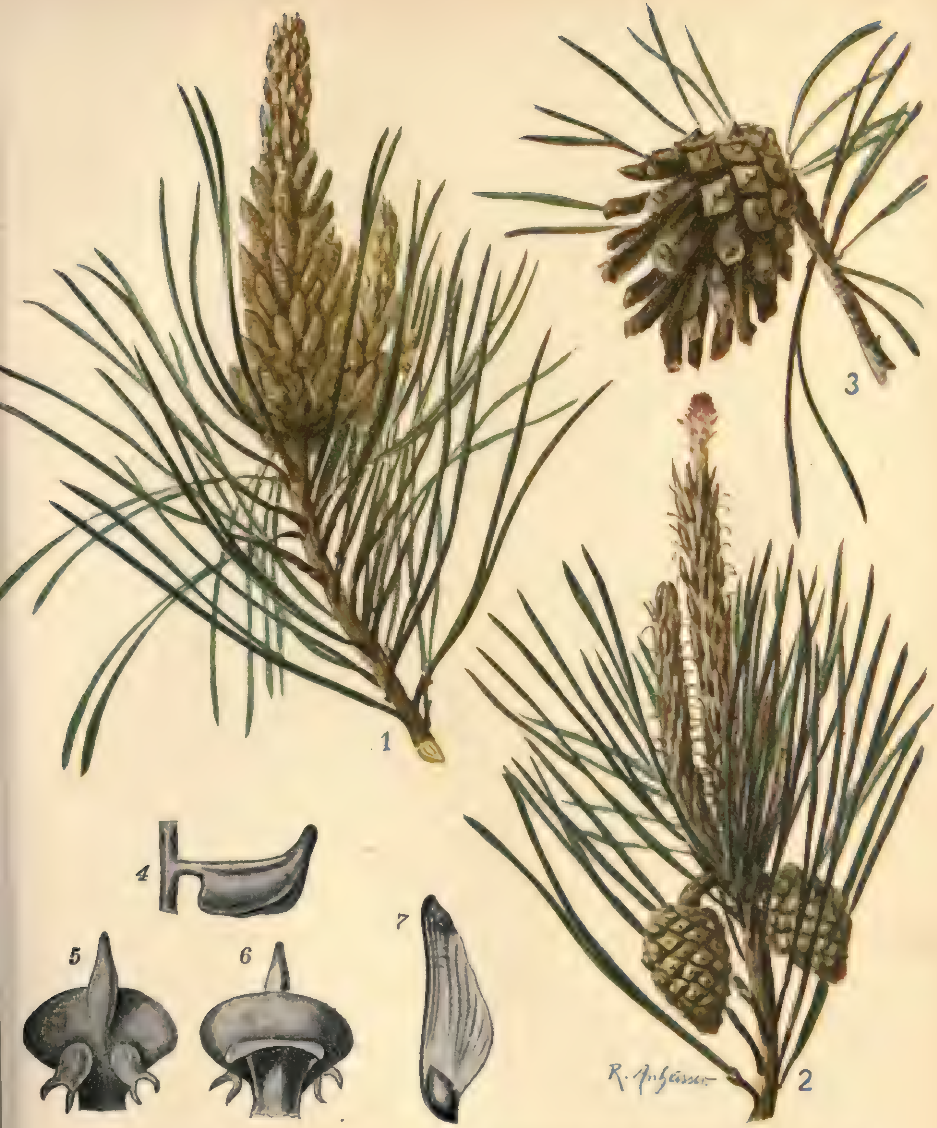


FIG. 464.—*Pinus silvestris* (⅔ nat. size). *1*, Shoot of unlimited growth bearing short shoots; at the top the shoot of the current year. At the base of the latter are numerous male flowers each in the place of a short shoot, and nearer the tip brown scale leaves, in the axil of each of which is a short shoot. *2*, Similar branch bearing a young female flower at the summit of the shoot of the current year, in place of a branch of unlimited growth. Two dependent green cones are borne on the shoot of the preceding year. *3*. Cone of the year before last, opened to allow of the escape of the seeds. *4*, A microsporophyll. *5*, Macrosporophyll from the adaxial side showing the ovuliferous scale with the two ovules at the base. *6*, Macrosporophyll from the abaxial side showing the small bract-scale below the large ovuliferous scale. *7*, Ripe seed with its wing derived from the superficial layers of the ovuliferous scale. (× 4-7.) *OFFICIAL.*

outer or lower surface is convex. The growing points of the short shoots soon become functionless unless stimulated to activity by the death of the apical bud. The male flowers appear in large numbers at the base of the long shoots of the current year and stand in place of the short shoots. One or several female flowers arise at the tip of similar long shoots, and each corresponds in position to a shoot of unlimited growth. At the time of flowering they are erect, but are bent downwards after pollination. The seeds ripen in the second year, and are set free by the separation of the scales of the cone which till then have been closely pressed together. The cones subsequently are shed (Fig. 464). *Pinus montana*, a dwarf Pine occurring on mountains; *P. pinea*, *P. cembra*, with edible seeds; *P. laricio*, Corsican Pine from Austria; *P. Pinaster*, Maritime Pine from the Mediterranean region; *P. taeda*, *P. Strobus*, Weymouth Pine, *P. Lambertiana* from N. America.

Cedrus.—Cedars from the forests on Atlas and Lebanon.

POISONOUS.—*Juniperus Sabina*, *Taxus baccata*.

OFFICIAL.—*Pinus sylvestris* and other species produce OLEUM TEREBINTHINAE and RESINA; *Abies balsamea* supplies TEREBINTHINA CANADENSIS; *P. palustris* and *P. taeda* yield THUS AMERICANUM; *P. excelsa* yields PIX BURGUNDICA; *P. sylvestris*, etc. PIX LIQUIDA; *P. pumilio*, OLEUM PINI; *Juniperus oxycedrus* and other species yield OLEUM CADINUM; *Juniperus communis*, OLEUM JUNIPERI.

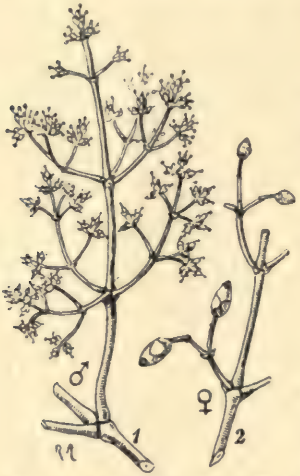


FIG. 465.—*Ephedra altissima*. *1*, Habit of a male inflorescence. *2*, An inflorescence with unripe fruits. (⅔ nat. size.)

Order 4. Gnetinae (8)

The only Family in this order is that of the **Gnetaceae,** to which only three genera belong; *Ephedra* (Fig. 465) leafless shrubs of warm dry regions of the Northern hemisphere; *Welwitschia mirabilis*, a monotypic plant from the deserts of South-West Africa; the widely expanded summit of the stem bears after the cotyledons only a single pair of leaves, which are 1 m. in length and continue to grow at their bases; *Gnetum* (Fig. 466), tropical trees or climbers with pairs of broad, reticulately veined leaves. These genera, while differing widely in appearance, agree in possessing opposite leaves (in *Ephedra* reduced to scales), in the development of vessels in the secondary wood, the absence of resin canals, and in the presence of a perianth to the flowers which are usually diœcious (Fig. 467).

These points of agreement with both Gymnosperms and Angiosperms make the group in many ways an intermediate one between the two classes. The development of the sexual generation in the three genera is as various as their external habit.

The microspores in their development and germination show no differences from those of other Gymnosperms. The macrospores of *Ephedra* and *Welwitschia* have

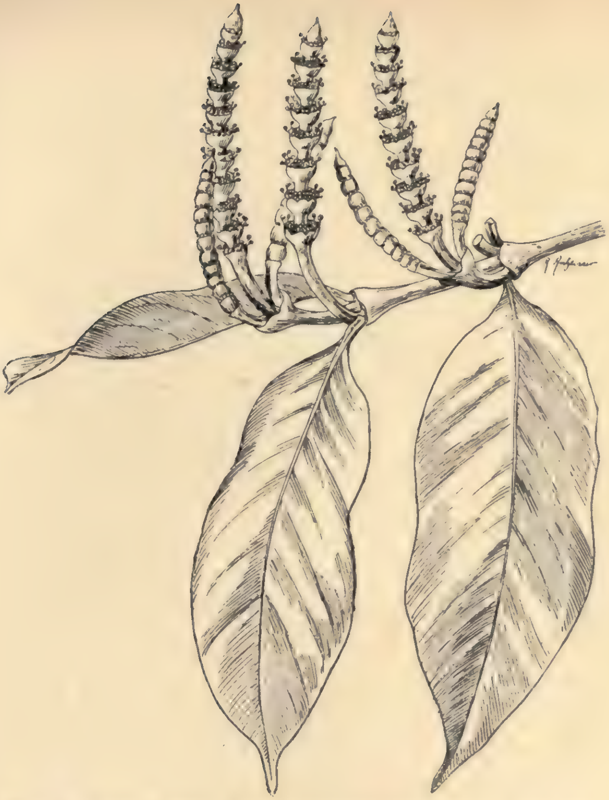


FIG. 466.—*Gnetum Gnemon.* Branch with male inflorescences. (½ nat. size.)

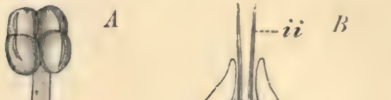


FIG. 467.—*A*, *Ephedra altissima.* Male flower. × 16; *pg*, perigone; *b*, leaf. *B*, *Gnetum Gnemon*, longitudinal section of a female flower (× 32. After LOTSY); *n*, nucellus; *ii*, inner, and *ai*, outer integuments; *pg*, integument-like investment or perianth.

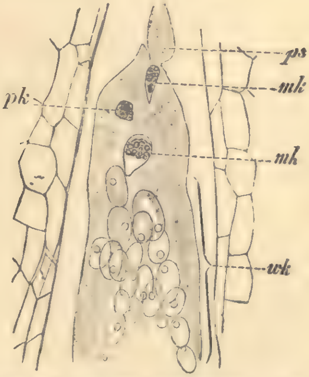


FIG. 468.—*Gnetum Rumphianum.* Apex of the embryo-sac shortly before the formation of the embryos. *wk*, female nuclei; *mk*, male nuclei; *ps*, pollen-tube; *pk*, disorganised nucleus of the pollen-tube. (× 250.)

well-developed prothallia; in the latter plant the archegonia are reduced to elongated cells penetrating the tissue of the nucellus. In *Gnetum*, on the other hand, either no prothallium is formed but the embryo-sac becomes filled with protoplasm in which are numerous nuclei, or a prothallium is developed in the lower portion of the embryo-sac while the upper portion contains protoplasm with free nuclei. Each of the two generative cells from the pollen-tube fuses with a female nucleus. Of all the fertilised cells resulting from the penetration of a number of pollen-tubes to the embryo-sac only one develops into an embryo (Figs. 468, 469).

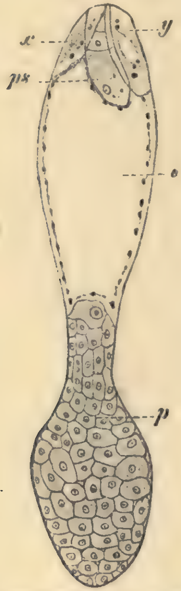


FIG. 469.—*Gnetum Gnemon*. Embryo-sac. *e*, upper portion with free nuclei; *p*, lower portion filled with the tissue of the prothallium; *ps*, pollen-tube; *x*, *y*, two arrested embryo-sacs. (× 66, after LOTSY.)

Fossil Gymnosperms (9)

In contrast to what was seen to be the case for the Pteridophyta, Gymnosperms have not yet been detected in Silurian strata. They appear first in the Devonian, but are sparingly represented and first form an important constituent of the flora in the Carboniferous. From the **Cycadofilices**, which possessed stems with secondary thickening and fern-like foliage and had been hitherto regarded as Pteridophyta, OLIVER and SCOTT (9a) have recently separated the **Pteridospermeae**; these may be briefly characterised as fern-like spermaphyta. They have shown that the seeds of *Lagenostoma Lomaxi*, Will, belong to *Lyginodendron*, one of the Cycadofilices with fern-like foliage, and that this plant must therefore be placed in the Pteridospermeae. It is highly probable that the whole of the Lyginopterideae and possibly of the Medulloseae also must be placed in this group. The structure of the seed of *Lagenostoma* resembles that of *Cycas*, but, instead of the single thick integument of the latter, had a cupular investment to the seed on the outside of the integument. In North America fragments of leaves referred to *Cordaites* have been found. This genus belongs to a peculiar type confined to the Palæozoic rocks. Owing to the excellence of the preservation of their remains the morphology of the Cordaiteae is as well known as that of the existing Gymnosperms. They were lofty trees with linear or broad and lobed leaves. Their flowers differ considerably from those of recent Gymnosperms. An important fact as bearing on the phylogeny of the group is the presence of a male prothallus as a small multicellular body. The ovules and seeds show great structural agreement with those of the Cycadaceae.

With the exception of some less common fossils (*Cycadites*, *Dicranophyllum*), the former of which is doubtfully referred to the Cycadinae, the latter more probably to the Ginkgoineae, *Cordaites* is the most richly represented type of Gymnosperm found in the Carboniferous rocks. Undoubted Cycadaceae make their appearance in the lower Rothliegende. In later strata the genus *Walchia*, of uncertain affinity, appears; the vegetative organs, which alone are known, recall the lowest Coniferae (Araucariaceae). In the upper Rothliegende undoubted

Ginkgoaceae (*Baiera*) make their appearance, with another type referred to the Coniferae (*Ullmannia*).

The Cordaiteae disappear in the Rothliegende. The Gymnosperm flora can be followed through the Trias, in which it consisted of extinct types of Cycadineae, Ginkgoineae, and Coniferae (*Voltzia*, in the Bunter Sandstone), to the Jurassic period. In the latter it attained a great development in that both the Ginkgoineae and the Cycadineae attained their maximum development and were represented by numerous forms. True Araucarieae also appear in the Jurassic; on this account, as well as on account of their organisation, this group may be regarded as the oldest of the existing Coniferae.

In the Wealden Cycadineae and Ginkgoineae, along with some Coniferae, were dominant among the Gymnosperms. On passing to the Cretaceous strata the ancient types are found to be reduced, while the Coniferae become more numerous. Among the latter existing genera appear (*Dammara*, *Sequoia*, *Pinus*, *Cedrus*, *Abies*, *Callitris*, etc.). The Taxaceae also appear to be represented, but the remains are of uncertain affinity.

The Tertiary Gymnosperms belong entirely to existing types and for the most part to existing species. The Coniferae are dominant; the Ginkgoineae are represented only by *Ginkgo biloba*, but this occurred in Europe along with other species now limited to Eastern Asia or North America (*Cryptomeria japonica*, *Taxodium distichum*, *T. heterophyllum*, *Sequoia gigantea*, *S. sempervirens*, *Pinus Strobus* etc.). One Cycadaceous plant (*Encephalartos*) is also known.

CLASS II

Angiospermae (10)

The differences between gymnospermic and angiospermic plants are well and shortly expressed by saying that the seeds of the former are naked, while those of the latter are enclosed in a cavity. Only a detailed account of the structure of the angiospermic flower will, however, make the relations existing between the two great classes of Phanerogams clear.

The Angiospermic Flower.—The male and female sporophylls of Gymnosperms were borne in distinct flowers or even on different individual plants, and the flowers had no special envelope. In Angiosperms, on the other hand, a union of the two sexes in the one flower which is thus HERMAPHRODITE and the investment of the flower by coloured leaves (differing in appearance from the foliage leaves) forming a PERIANTH is the rule. In contrast to the UNISEXUAL or DICLINOUS flower with the sporophylls arranged spirally on an elongated axis, which is characteristic of the Gymnosperms, the perianth leaves and sporophylls in the Angiosperms are usually borne in whorls on a greatly shortened axis. THE ARRANGEMENT OF THE FLORAL LEAVES IN WHORLS, THE COLOURED PERIANTH, AND THE HERMAPHRODITE NATURE OF THE FLOWERS ARE THUS CHARACTERISTIC

OF ANGIOSPERMS, although these features do not apply without exceptions to all angiospermic flowers. These differences depend on the important factor of the MEANS OF POLLINATION. When, as is the case with the Gymnosperms and the catkinate flowers of Angiosperms, this function is performed by the wind, the elongation of the axis and the absence of an investment of leaves around the female receptive organ are advantageous. When, on the other hand, pollination is effected by insects or birds, the conspicuousness given by the presence of a perianth and other attractions, such as scent or sweet-tasting substances, are necessary. The form of the flower, the arrangement of the sporophylls in it, and the place at which nectar is secreted must be adapted to the visiting insects (cf. p. 308). It is to this, that the variety of form and colour exhibited in the flowers of Angiosperms must be ascribed. According to the means of pollination, anemophilous, entomophilous, ornithophilous etc. flowers are distinguished.

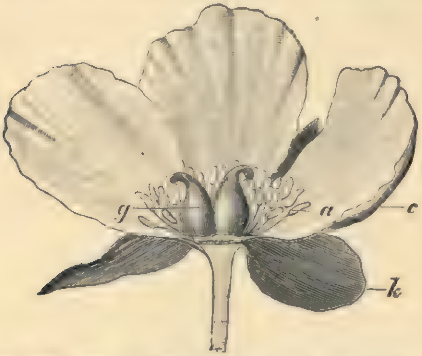


FIG. 470.—Flower of *Paeonia peregrina*, in longitudinal section. *k* and *c*, Perianth ; *a*, androecium ; *g*, gynaeceum. (½ nat. size.)

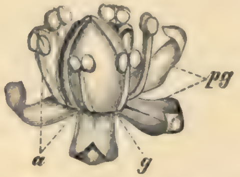


FIG. 471.—Flower of *Acorus Calamus*. *pg*, perigone ; *a*, androecium ; *g*, gynaeceum. (Enlarged. After ENGLER.)

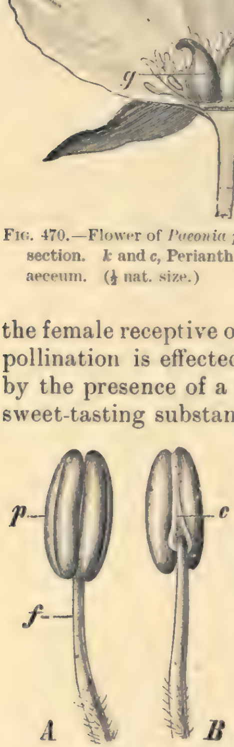


FIG. 472.—*A* and *B*, anterior and posterior view of a stamen of *Hyoscyamus niger* ; *f*, the filament ; *p*, anther ; *c*, connective (magnified).

The perianth (Figs. 470, 471) consists of two whorls of members : these may be similar in form and colour, when the name PERIGONE is given to them, or may be differentiated into an outer green CALYX and an inner whorl of coloured leaves, the COROLLA. In every complete flower two whorls of stamens or microsporophylls come next within the perianth, and within these again a whorl of carpels or macrosporphylls. The whorls alternate regularly with one another. The stamens collectively form the ANDROECIUM, the carpels the GYNAECEUM.

Each stamen consists of a cylindrical stalk or FILAMENT and of the ANTHER ; the latter is formed of two THECÆ or pairs of pollen-sacs joined by the continuation of the filament, the CONNECTIVE (Fig. 472). According to whether the thecæ are turned inwards, *i.e.* towards the whorl of carpels, or outwards, the anther is described as INTRORSE or EXTRORSE. The opening of the ripe theca depends as a rule (except in the Ericaceae) on the peculiar construction of the hypodermal layer of the wall of the pollen-sac. This is called the fibrous layer or ENDOTHECIUM. On the other hand, in the Gymnosperms (excluding *Ginkgo*, cf. p. 488), as in the Ferns, the dehiscence is effected by means of the external layer of cells (exothecium). As a rule the septum between the two pollen-sacs breaks down, so that they are both opened by the one split in the wall. The microspores in anemophilous plants are smooth, dry and light, and adapted for distribution by the wind. In entomophilous flowers, on the other hand, the exine is frequently sticky or provided with spiny projections, and the pollen-grains are thus enabled to attach themselves better to the bodies of the insect visitors. They also differ from the pollen-grains of the Gymnosperms in having more or less numerous spots in the wall prepared beforehand for the emission of the pollen-tube (Figs. 473, 474). Various modifications of the androecium result from the cohesion, and branching of the stamens, and will be described in the special part. Sterile stamens which do not produce fertile pollen are termed STAMINODES.

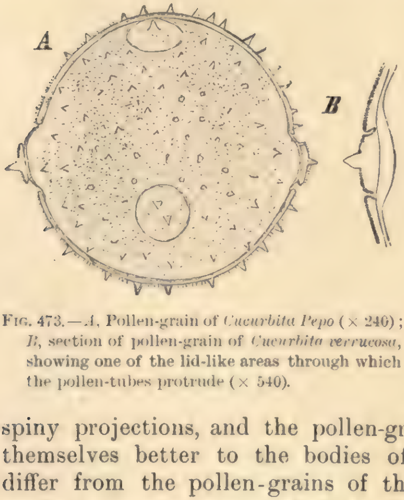


FIG. 473.—*A*, Pollen-grain of *Cucurbita Pepo* (× 240); *B*, section of pollen-grain of *Cucurbita verrucosa*, showing one of the lid-like areas through which the pollen-tubes protrude (× 540).

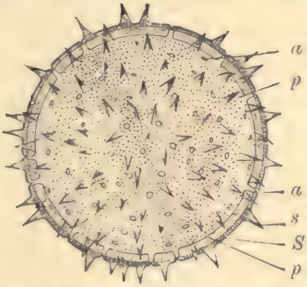


FIG. 474.—Pollen-grain of *Malva silvestris*. *S*, Spinous projections of the exine; *s*, vertically striated layer of the exine; *p*, the same seen from above; *a*, places of exit of pollen-tubes. (After A. MEYER.)

The flower is terminated above by the GYNAECEUM. The CARPELS composing this may remain free and each give rise to a separate fruit (APOCARPOUS GYNAECEUM) or they unite together to form the ovary (SYNCARPOUS GYNAECEUM). The carpels, as in the Cycadaceae, as a rule bear the ovules on their margins, on more or less evident outgrowths which are termed PLACENTAS. In apocarpous gynaecea the ovules are thus borne on the united margins of the carpels, each margin bearing a row of ovules (Fig. 476). This is termed the

VENTRAL SUTURE, while the midrib of the carpel forms the DORSAL SUTURE. In syncarpous ovaries the ovules are similarly borne on the margins of the coherent carpels. The placentation is termed PARIETAL when the placentas form projections from the inner surface of the wall of the ovary (Fig. 477 D). If the margins of the carpels project farther into the ovary, and divide its cavity into chambers or loculi, the placentas are correspondingly altered in position, and the placentation becomes AXILE (Fig. 477 B). In contrast to such TRUE SEPTA, formed of the marginal portions of the carpels, those that arise as outgrowths of the surface or sutures of the carpels, as in the Cruciferae, are called FALSE SEPTA. By the upgrowth of the floral axis in the centre of the ovary what is known as FREE CENTRAL PLACENTATION comes about. The projecting axis cannot be sharply distinguished from the tissue of the carpels. The septa, which were originally present, are arrested at an early stage of development or completely disappear, so that the ovules are borne on the central axis covered with carpellary tissue and enclosed in a wall formed by the outer portions of the carpels.

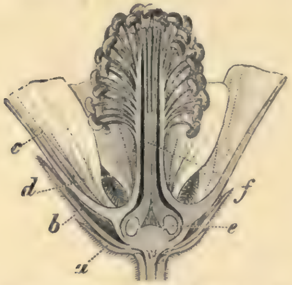


FIG. 475.—*Althaea officinalis*, flower cut through longitudinally; *a*, epicalyx; *b*, calyx; *c*, corolla; *d*, androecium. (After BERG and SCHMIDT, magnified.)

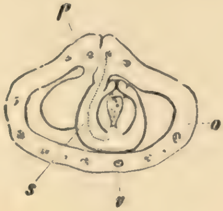


FIG. 476.—Transverse section of an ovary of *Delphinium Ajacis*, showing ovule placed horizontally; *s*, ovule; *p*, placenta; *o*, wall of ovary; *v*, vascular bundles. (× 18.)

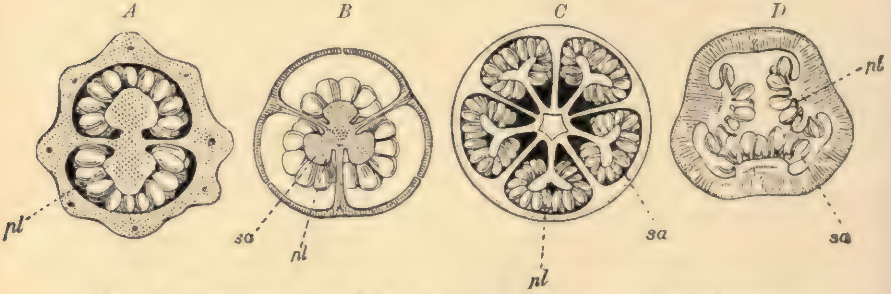


FIG. 477.—Transverse sections of ovaries. *A*, *Lobelia*; *B*, *Diapensia*; *C*, *Rhododendron*; *D*, *Passiflora*; *pl*, placenta; *sa*, ovules. (After LE MAOUT and DECAISNE.)

Each carpel usually is prolonged above into a a stalk-like STYLE terminating in a variously shaped STIGMA. The stigma serves as the receptive apparatus for the pollen, and in relation to this is often papillate or moist and sticky (Fig. 478 D). When the gynaeceum is completely syncarpous, it has only one style and stigma. In

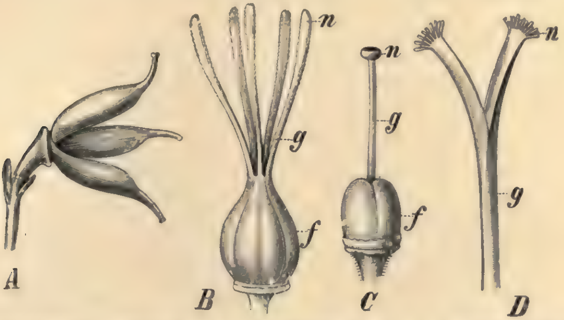


FIG. 478.—Different forms of gynaecea. *A*, Of *Aconitum Napellus*; *B*, of *Linum usitatissimum*; *C*, of *Nicotiana rustica*; *D*, style and stigma of *Achillea Millefolium*; *f*, ovary; *g*, style; *n*, stigma. (After BERG and SCHMIDT, magnified.)

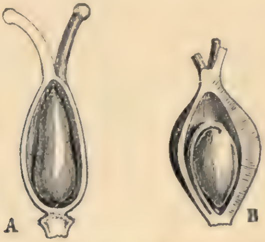


FIG. 479.—Ovaries containing basal ovules shown in longitudinal section. A, *Fagopyrum esculentum* (atropous); B, *Armeria maritima* (anatropous). (After DUCHARTRE. × 20.)

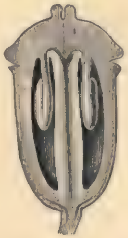


FIG. 480.—Ovary of *Foeniculum officinale* with pendulous ovules, in longitudinal section. (After BERG and SCHMIDT, magnified.)

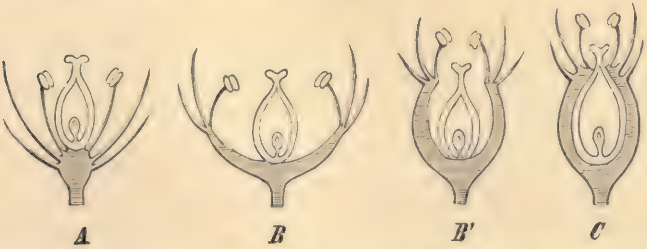


FIG. 481.—Diagram of (*A*) hypogynous (*B*, *B′*), perigynous, and (*C*) epigynous flowers.

Fig. 478 an apocarpous (*A*) and a syncarpous gynaeceum (*C*) are represented, together with one in which the carpels are coherent below to form the ovary while the styles are free (*B*).

The POSITION OF THE OVULES WITHIN THE OVARY may be erect, pendulous, horizontal, or oblique to the longer axis (Figs. 479, 480). In anatropous ovules the raphe is said to be ventral when it is turned towards the ventral side of the carpel, and dorsal if towards the dorsal side of the carpel.

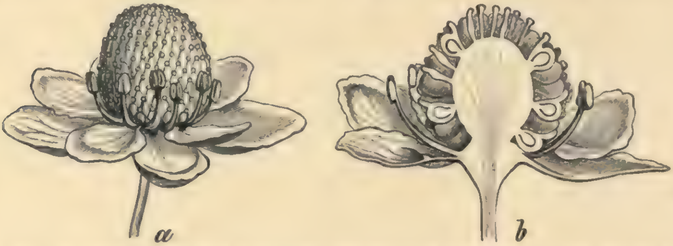


FIG. 482.—Hypogynous flower of *Ranunculus sceleratus* with numerous, superior ovaries borne upon a club-shaped receptacle. (After BAILLON, magnified.)

The differences in the form of the floral axis, which involve changes in the position of the gynaeceum, lead to differences in the form of the flower itself. Some of the commonest cases are diagrammatically represented in Fig. 481 *A-C*. The summit of the floral axis is usually thicker than the stalk-like portion below; it is often widened out and projecting, or it may be depressed and form a cavity. If the whorls of members of the flower are situated above one another on a simple, conical axis THE GYNAECEUM FORMS THE UPPERMOST WHORL AND IS SPOKEN OF AS SUPERIOR, WHILE THE FLOWER IS TERMED HYPOGYNOUS (Figs. 482, 483). If, however, the end of the axis is expanded into a flat or cup-shaped receptacle, an interval thus separating the androecium and gynaeceum, the flower is termed PERIGYNOUS

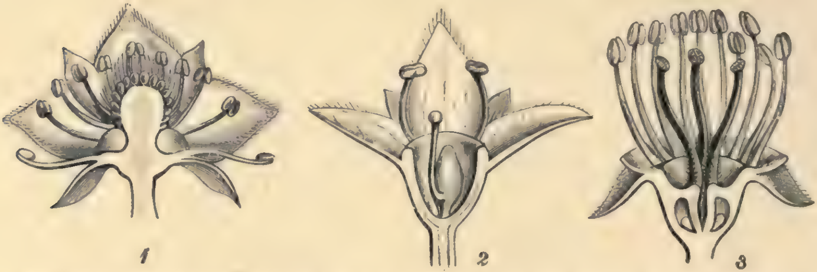


FIG. 483.—Different flowers belonging to the family Rosaceae, cut through longitudinally. *1*, *Potentilla palustris*, hypogynous; *2*, *Alchemilla alpina*, perigynous; *3*, *Pyrus Malus*, epigynous. (After FOCKE in *Nat. Pflanzen-familien*, magnified.)

(Fig. 483, 2). When the concave floral axis, the margin of which bears the androecium, becomes adherent to the gynaeceum, the latter is said to be INFERIOR while the flower is described as EPIGYNOUS.

The regions of the axis or of other parts of the flower which excrete a sugary solution to attract the pollinating animal visitors are called NECTARIES. Their biological importance is considerable.

In a typical angiospermic flower the organs are thus arranged in five alternating whorls, of which two comprise the perianth, two the androecium, while the gynaeceum consists of one whorl. The flower is PENTACYCLIC. The number of members is either the same in each whorl (*e.g.* three in a typical Monocotyledon flower, or five in a typical Dicotyledon flower), or an increase or decrease in the number takes place. This is especially the case with the whorls composing the androecium and gynaeceum.

Some of the more frequent deviations from the floral structure described above may be referred to here. Variation in the number of whorls is common. A diminution in the number may result from the absence of one kind of sexual organ in diclinous flowers (*e.g. Myristica*), or from the absence of one of the two whorls composing the androecium or perianth (Compositae). Flowers in which the androecium consists of only one whorl are termed HAPLOSTEMONOUS, those with two whorls of stamens DIPLOSTEMONOUS. On the other hand, the number of whorls may be increased, and this may affect the androecium (*Rosa*), the gynaeceum (*Punica granatum*), or the perianth (*Hagenia abyssinica*). Another simple modification concerns the position of the whorls. The outer whorl of the androecium, in *Erica*, for instance, does not alternate with the segments of the corolla but the stamens stand directly above the latter. Such an androecium is distinguished as OBDIPLOSTEMONOUS from the ordinary DIPLOSTEMONOUS type.

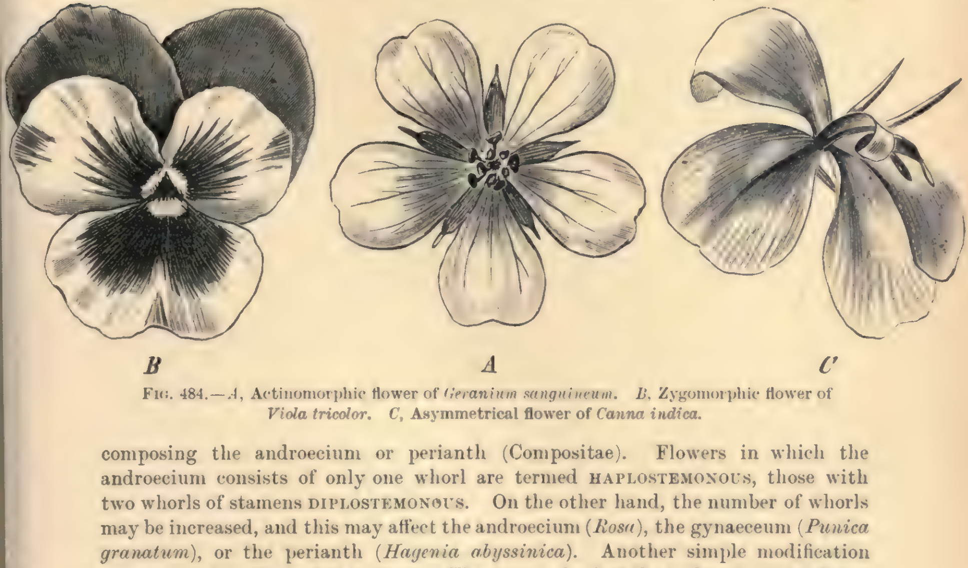


FIG. 484.—*A*, Actinomorphic flower of *Geranium sanguineum*. *B*, Zygomorphic flower of *Viola tricolor*. *C*, Asymmetrical flower of *Canna indica*.

Variations in floral symmetry are more important both biologically and with regard to the general habit of the flower. Those flowers which can be divided into similar halves by more than two planes passing through the axis are termed RADIALLY SYMMETRICAL or ACTINOMORPHIC (Fig. 484 *A*). When a symmetrical division can only be made by two such planes of section the flower is BISYMMETRICAL or BILATERAL (*e.g. Dicentra*, belonging to the Fumariaceae). From the originally radial type the DORSIVENTRAL (SYMMETRICAL, ZYGOMORPHIC), and the ASYMMETRICAL types can be derived by the unequal size of some of the members or their displacement or suppression (Fig. 484 *B*, *C*; cf. p. 16). In zygomorphic flowers there is only one plane of symmetry by which the flower can be divided into corresponding halves; while in asymmetrical flowers no such plane of symmetry exists. Dorsiventral flowers tend to take up a particular position in relation to the directive force of gravity and exhibit a high degree of adaptation to insect pollination. According to whether the plane of symmetry coincides with the MEDIAN PLANE of the flower (*i.e.* the plane passing through the axis of the flower and the main axis), forms an acute angle with the median plane, or is at right angles to it, flowers are distinguished as MEDIANLY DORSIVENTRAL, OBLIQUELY DORSIVENTRAL, or TRANSVERSELY DORSIVENTRAL respectively (Fig. 485). Radially symmetrical monstrosities of normally zygomorphic flowers are termed PELORIC.

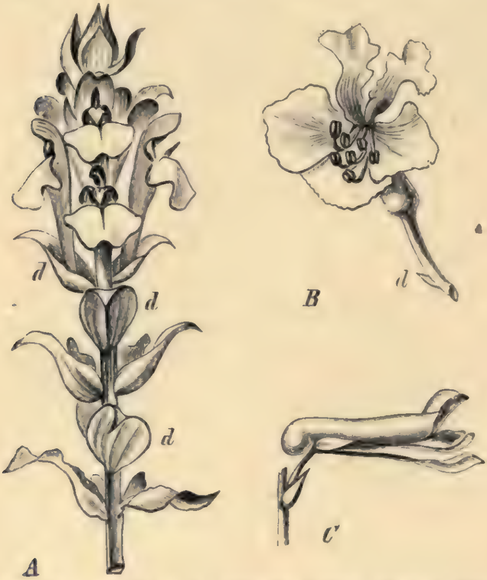


FIG. 485.—Flowers of, *A*, *Scutellaria alpina*, medianly zygomorphic (dorsiventral); *B*, *Aesculus hippocastanum*, obliquely zygomorphic (dorsiventral); *C*, *Corydalis lutea*, transversely zygomorphic (dorsiventral); *d*, bracts.

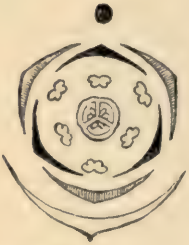


FIG. 486.—Diagram of a pentacyclic flower (*Lilium*).

If a diagram of the arrangement of the members as they are seen in a cross section of an opened flower-bud is constructed (p. 16) and so oriented that the transverse section of the axis of the inflorescence stands above, that of the bract below the ground plan of the flower, what is known as a FLORAL DIAGRAM is obtained. The accompanying floral diagram (Fig. 486) is that of a monocotyledonous flower with five whorls of members. A FLORAL FORMULA gives a short expression for the members of a flower as shown in the floral diagram. Denoting the calyx by K, the corolla by C (if the perianth forms a perigone it is denoted by P), the androecium by A, and the gynaeceum by G, the number of members in each case is placed after the letter. Thus the floral formula of the monocotyledonous flower represented in Fig. 486 would be, P 3 + 3, A 3 + 3, G 3. When there is a large number of members in a whorl the symbol ∞ is used denoting that the number is large or indefinite. Such a formula may be further made to denote the cohesion of the members of a whorl by enclosing the proper number within brackets, and by placing a horizontal line below or above the number of the carpels the superior or inferior position of the ovary is expressed. By placing an arrow before the formula the dorsiventrality of the flower may be indicated, and by varying the direction of the arrow it can be made clear whether the dorsiventrality is median, oblique, or transverse. The formula for the Lily given above and for a number of other flowers would thus take the following forms :—

Lily. $P\,3+3,\ A\,3+3,\ G\,\underline{(3)}.$

Buttercup. $K\,5,\ C\,5,\ A\,\infty,\ G\,\underline{\infty}.$

Laburnum. $\downarrow K\,5,\ C\,5,\ A\,(5+5),\ G\,\underline{1}.$

Hemlock. $K\,5,\ C\,5,\ A\,5,\ G\,(\overline{2}).$

Artemisia. $K\,0,\ C\,(5),\ A\,(5),\ G\,(2).$

Inflorescence.—In many Angiosperms the single flowers are borne in large numbers on special branch systems which differ in a number of respects from the vegetative branch systems and are termed INFLORESCENCES. In inflorescences, as in the vegetative region (cf. p. 20), branches usually arise only from the leaf-axils, the subtending leaf being termed a BRACT. Leaves borne on the axis of the flower itself are known as BRACTEOLES. Bracts and bracteoles may be classed together as BRACTEAL LEAVES (Fig. 487). The MEDIAN PLANE passes through the axis and the middle line of the bract. The bracteoles, and the branches produced from their axillary buds, may lie in this median plane when they are said to have a MEDIAN POSITION, or more commonly they stand right and left of it, and their position is described as TRANSVERSE (Fig. 487).

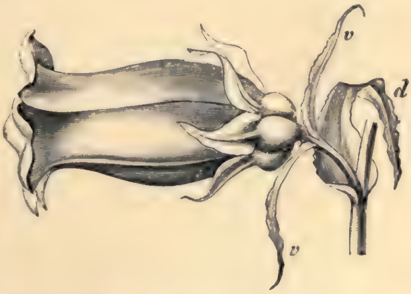


FIG. 487. Flower of *Campanula medium* with bract (*d*) and bracteoles (*v*).

According to the relative development of the main and lateral axes in an inflorescence a distinction is made between RACEMOSE inflorescences, in which the main axes are strongly developed and exceed their lateral shoots, and CYMOSE inflorescences in which the lateral axes are more strongly developed and overtop the main axis. The former may be also termed MONOPODIAL in contrast to the SYMPODIAL or cymose type. The more frequent kinds of inflorescence are enumerated below.

I. Racemose Inflorescences.

(*a*) Lateral axes unbranched.

1. RACEME ; stalked flowers borne on an elongated main axis (Figs. 488 *A*, 489).
2. SPIKE ; flowers sessile on an elongated main axis (Figs. 488 *B*, 490). A spike in which the axis is thickened and succulent is termed a SPADIX ; a spike which, after flowering or after the fruits have ripened, falls off as a whole, is a CATKIN (Fig. 491).
3. UMBEL ; flowers stalked, on a shortened main axis (Figs. 488 *C*, 492).

4. Capitulum or head; flowers sessile, on a shortened main axis (Fig. 488 *D*).
   (*b*) lateral axes branched.
5. Panicle; a main axis bearing racemes laterally (Figs. 488 *E*, 493).

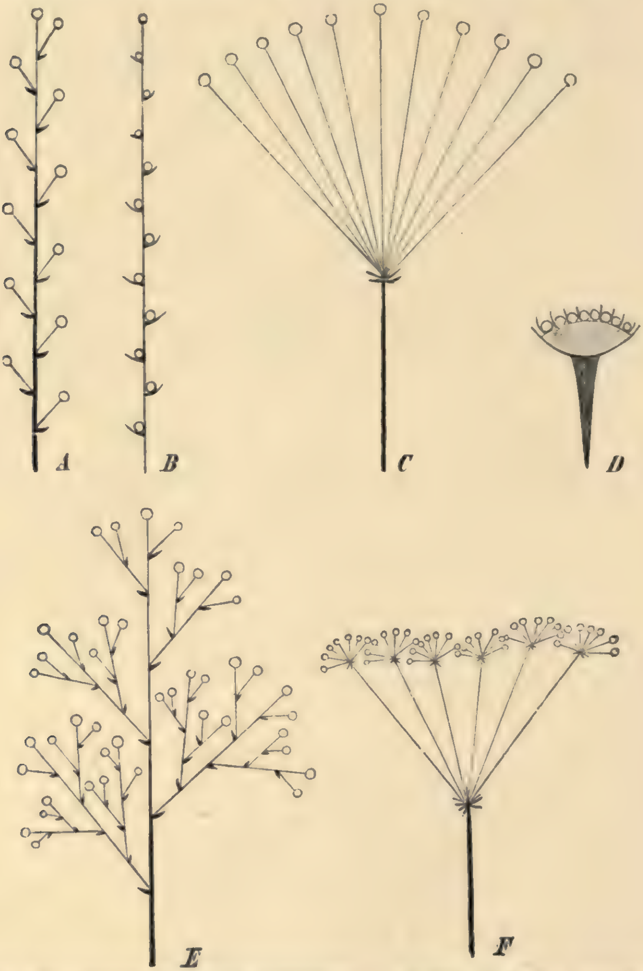


Fig. 488.—Diagrams of racemose inflorescences. *A*, Raceme. *B*, Spike. *C*, Umbel. *D*, Capitulum. *E*, Panicle. *F*, Compound umbel.

6. Compound umbel; an umbel bearing small umbels in place of the single flowers (Fig. 488 *F*).

II. Cymose Inflorescences.

(*a*) The relatively main axis bearing more than two lateral branches; Pleiochasium.

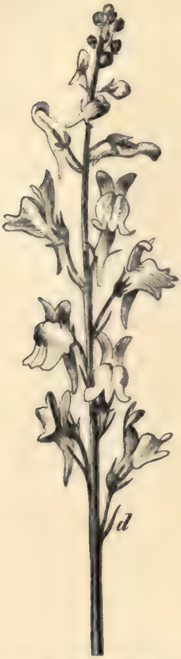


FIG. 489.—Raceme of *Linaria striata*. *d*, bracts.

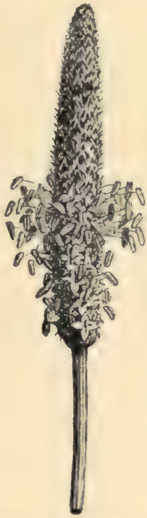


FIG. 490.—Spike of *Plantago lanceolata*. (After DUCHARTRE.)

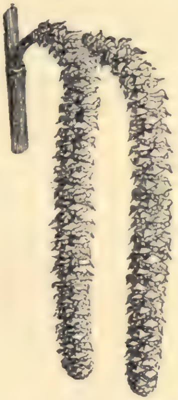


FIG. 491.—Catkin of *Corylus americana*. (After DUCHARTRE.)

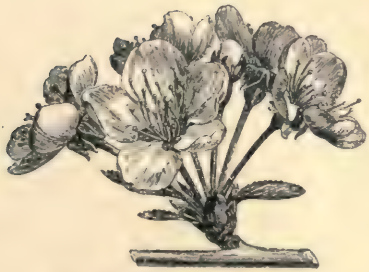


FIG. 492.—Umbel of the Cherry. (After DUCHARTRE.)

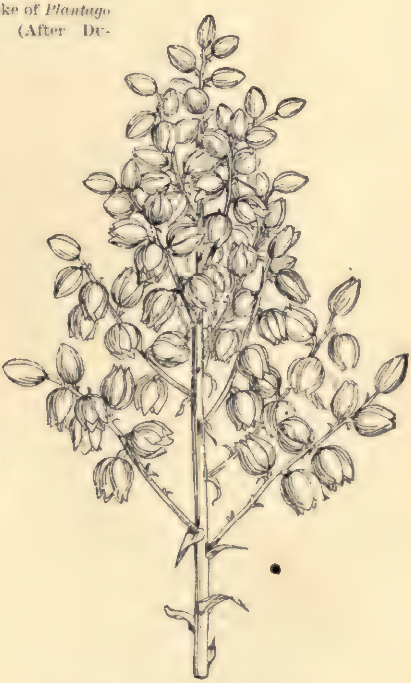


FIG. 493.—Panicle of *Yucca filamentosa*. (Reduced.)

(*b*) Each relatively main axis bears two lateral branches ; DICHASIUM (Figs. 494 *E*, 495).

(*c*) Each relatively main axis bears one lateral branch ; MONOCHASIUM.

1. **The successive lateral axes all fall in the median plane.**

(*α*) all the branches arise on the same side ; DREPANIUM (Fig. 494 *C*, *D*).

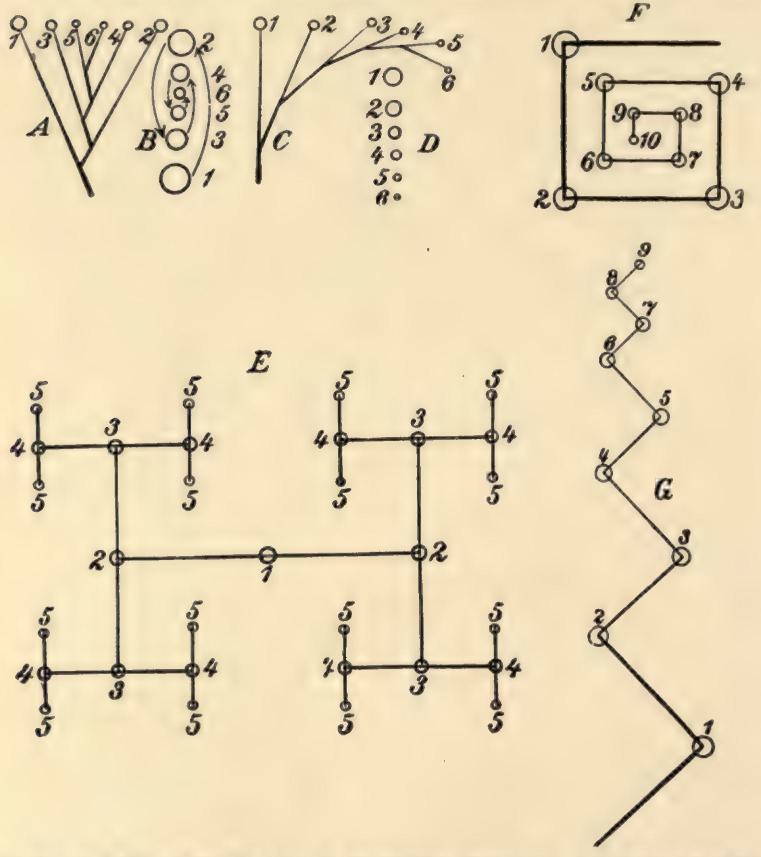


FIG. 494.—*A*, Rhipidium from the side ; *B*, rhipidium in ground plan *C*, Drepanium from the side ; *D*, ground plan of drepanium ; *E*, ground plan of dichasium ; *F*, ground plan of bostryx ; *G*, ground plan of cincinnus. *1-10*, successive, relatively main axes. (*A-D*, after EICHLER.)

(*β*) branches alternately right and left ; RHIPIDIUM (Fig. 494 *A*, *B* ; Fig. 546, *Iris*).

2. The lateral axes are transverse to the relatively main axis ; their arrangement can thus only be shown in ground plan.

(*α*) lateral axes always falling on the same side of the relatively main axis ; BOSTRYX (Fig. 494 *F*).

(*β*) lateral axes falling alternately on opposite sides of the relatively main axis ; CINCINNUS (Fig. 494 *F*, Fig. 496, a double cincinnus).

The Development of the Sexual Generation in the Angiosperms (11).—On germination the MICROSPORES of Angiosperms form an antheridial mother-cell (Fig. 497 *m*) which is clearly delimited from the large pollen-tube cell, but is not enclosed by a cell wall. The antheridial cell passes into the pollen-tube, and sooner or later divides into two generative cells (Fig. 497 *g*). The nucleus of the pollen-tube (*k*) is usually visible in the neighbourhood of the generative cells. The absence of the small prothallial cells, and of a sterile sister-cell of the antheridium, as well as the absence of a cell wall from the mother-cell of the antheridium, are points in which the Angiosperms differ from Gymnosperms. The reduction of the male prothallium has thus gone so far that only the indispensably necessary parts remain.

The characteristic differences which the Angiosperms show from the general course of development of the MACROSPORANGIUM in the Phanerogams commence with the

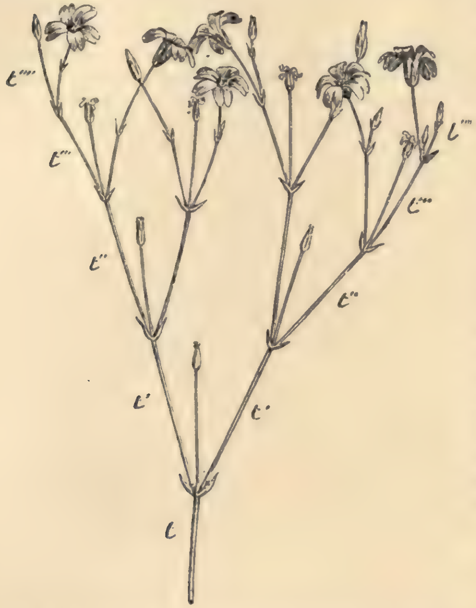


FIG. 495.—Cymose inflorescence (dichasium) of *Cerastium collinum*; *t*-*t''''*, successive axes. (After DUCHARTRE.)

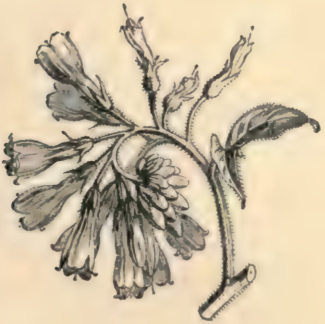


FIG. 496.—Scorpioid cyme of *Symphytum asperrimum*. (After DUCHARTRE.)

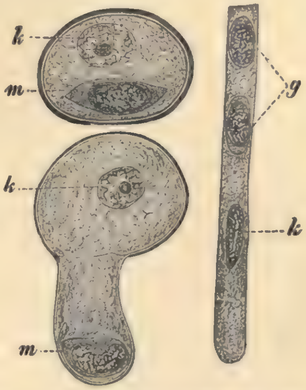


FIG. 497.—Pollen-grain of *Lilium Martagon* and its germination. *k*, Nucleus of the large vegetative cell of the pollen-tube; *m*, small mother-cell of the antheridium; *g*, generative cells. (After GUIGNARD. × 375.)

cell divisions in the single, functional macrospore-mother-cell resulting from the tetrad division (Fig. 498). The "PRIMARY NUCLEUS of the embryo-sac" divides and the daughter-nuclei separate from one another. They divide twice in succession so that eight nuclei are present. After this cell-formation commences around these nuclei. Both at the upper or micropylar end of the embryo-sac and at the lower end three naked cells are thus formed. The two remaining "POLAR NUCLEI" move towards one another in the middle of the embryo-sac, and fuse to form the "SECONDARY NUCLEUS of the embryo-sac." The three cells at the lower end are called the ANTIPODAL CELLS; they correspond to the vegetative prothallial cells, which in Gymnosperms fill the cavity of the embryo-sac, and in *Gnetum Gnemon* form a mass of tissue filling the lower end of the latter. The three cells at the micropylar end constitute the EGG-APPARATUS. Two of them are similar and are termed the SYNERGIDÆ, while the third, which projects farther into the cavity, is the EGG-CELL or OVUM itself. The synergidæ assist in the passage of the contents of the pollen-tube into the embryo-sac. Here also the process of reduction has gone as far as possible; in place of the more or less numerous archegonia of the gymnospermous macrospore only a single egg-cell is present. The significance of the synergidæ is difficult to determine unless they are regarded as archegonia which have become sterile.

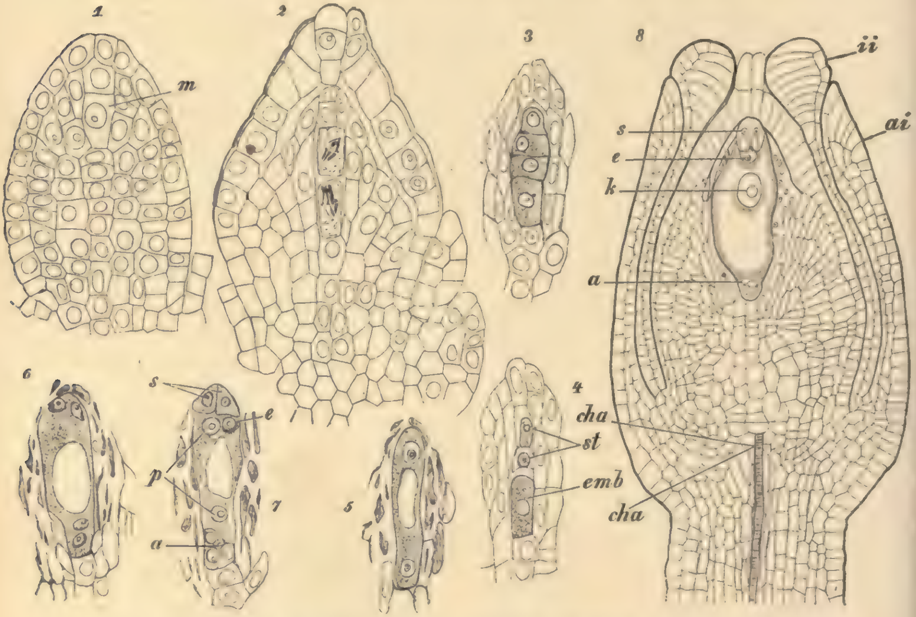


FIG. 498.—Development of the embryo-sac in *Polygonum divaricatum*. *m*, Mother-cell of the embryo-sac; *emb*, embryo-sac; *st*, sterile sister-cells; *e*, egg-cell; *s*, synergidæ; *p*, polar-nuclei; *a*, antipodal cells; *k*, secondary nucleus of the embryo-sac; *cha*, chalaza; *mi*, micropyle; *ai*, *ii*, outer and inner integuments; *fun*, funiculus. (*1-7* × 320, *8* × 135.)

The microspores, which cannot reach the macrospore directly, germinate on the stigma. The pollen-tube penetrates for the length of the style and as a rule the tip enters the micropyle of an ovule and so reaches the apex of the nucellus. Of late years a number of exceptions to this usual course have become known. Treub first showed in *Casuarina* that the pollen-tube entered the ovule by way of the chalaza, and thus reached the peculiar sporogenous tissue, which in this case develops a number of embryo-sacs. CHALAZOGAMY, as this mode of fertilisation is termed in contrast to POROGAMY, has no special systematic significance, since it is found to occur in numerous and unrelated plants. As NAWASCHIN has shown in the case of *Ulmus*, the pollen-tube in all these plants attempts to avoid growing across hollow cavities, possibly because it needs to be continually nourished at the expense of the surrounding tissue. A fuller understanding of chalazogamy and related phenomena is approached if they are regarded from this biological point of view (Figs. 499-501).

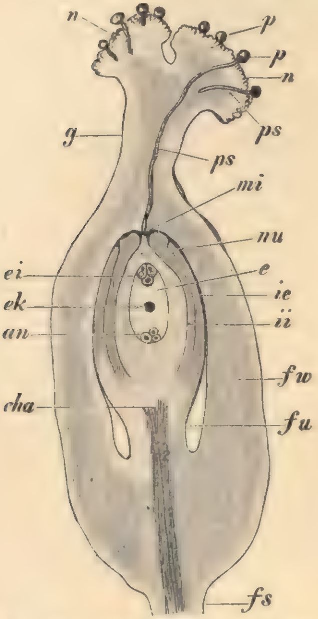


FIG. 499.—Ovary of *Polygonum Convolvulus* during fertilisation. *fs*, Stalk-like base of ovary ; *fu*, funiculus ; *cha*, chalaza ; *nu*, nucellus ; *mi*, micropyle ; *ii*, inner, *ie*, outer integument ; *e*, embryo-sac ; *ek*, nucleus of embryo-sac ; *ei*, egg-apparatus ; *an*, antipodal cells ; *g*, style ; *n*, stigma ; *p*, pollen-grains ; *ps*, pollen-tubes. (× 48.)

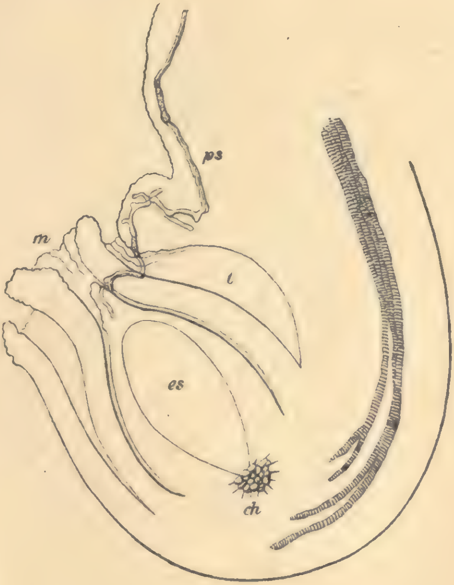


FIG. 500.—Ovule of *Ulmus pedunculata*. *es*, Embryo-sac ; *m*, micropyle ; *ch*, chalaza ; *t*, pocket-like space between the integuments. The pollen-tube, *ps*, penetrates directly through the two integuments and reaches the apex of the nucellus. (After NAWASCHIN.)

When the pollen-tube, containing the two generative cells, has reached the embryo-sac, its contents escape and pass by way of one of the synergidæ to the ovum ; the corresponding synergida then dies. One of the two generative nuclei fuses with the nucleus of the ovum, which then becomes surrounded by a cellulose wall. The second generative nucleus passes the ovum and unites with the large secondary nucleus of the embryo-sac to form the ENDOSPERM NUCLEUS (Figs. 502-504). Both the male nuclei are often spirally curved like a cork-screw, and NAWASCHIN, who first demonstrated the behaviour of the second generative nucleus, compares them to the spermatozoids of the Pteridophyta. The further development usually commences by the division of the endosperm nucleus, from which a large number of nuclei lying in the protoplasm lining the wall of the embryo-sac are derived. The endosperm arises by the formation of cell walls around these nuclei and their proper surrounding protoplasm, and by the increase in number of the cells thus formed (Fig. 95) to produce a massive tissue. The distinctive feature of the development of the endosperm in Angiosperms from the prothallus of Gymnosperms lies in the interruption which occurs in the process in the case of the endosperm. In the embryo-sac, when ready for fertilisation, only an indication of the prothallus exists in the vegetative, antipodal cells. The true formation of the endosperm is dependent on the further development of the embryo-sac, and waste of material is thus guarded against. The starting-point of this endosperm formation is given by the secondary nucleus of the embryo-sac, which needs to be stimulated by fusion with the second generative nucleus (the so-called vegetative fertilisation) to form the endosperm nucleus, before it enters on active division.

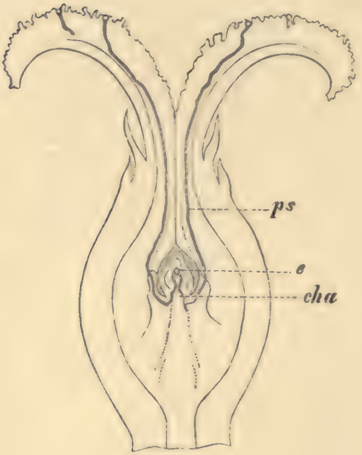


FIG. 501.—Longitudinal section of an ovary of *Juglans regia* to show the chalazogamy. *ps*, pollen-tube; *e*, embryo-sac; *cha*, chalaza. (Somewhat diagrammatic. × 6.)

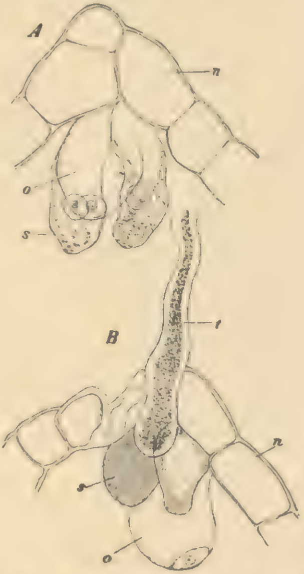


FIG. 502.—*Funkia ovata*. Apex of nucellus, showing part of embryo-sac and egg-apparatus. *A*, Before, *B*, during fertilisation; *o*, egg-cell; *s*, synergidæ; *t*, pollen-tube; *n*, nucellus. (× 390.)

From the fertilised ovum enclosed within its cell wall a PRO-EMBRYO consisting of a row of cells is first developed; the end cell of this row gives rise to the greater part of the EMBRYO. The rest of the pro-embryo forms the SUSPENSOR. Between the embryo and suspensor is a cell known as the HYPOPHYSIS, which takes a small part in the formation of the lower end of the embryo. The segmentation of the embryo presents differences according to whether the plant belongs to the Monocotyledons or Dicotyledons. IN THE LATTER TWO COTYLEDONS ARE FORMED AT THE END OF THE GROWING EMBRYO (FIG. 505), AND THE GROWING POINT OF THE SHOOT ORIGINATES AT THE BASE OF THE DEPRESSION BETWEEN THEM. MONOCOTYLEDONS, ON THE OTHER HAND, HAVE A SINGLE LARGE TERMINAL COTYLEDON, THE GROWING POINT BEING SITUATED LATERALLY (Fig. 506). In both cases the root is formed from the end of the embryo which is directed towards the micropyle ; its limits can be readily traced in older embryos, and it can be seen that a few cells are derived from the hypophysis adjoining the embryonic cell.

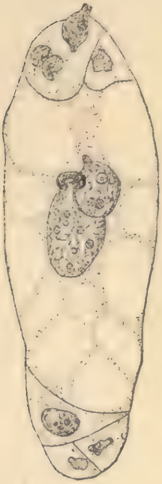


FIG. 503.—Fertilisation of *Lilium Martagon*. One of the male nuclei is close to the nucleus of the ovum, the other is in contact with the nuclei of the embryo-sac. (After GUIGNARD.)

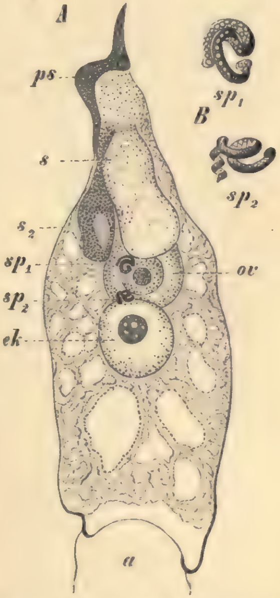


FIG. 504.—*A*, Embryo-sac of *Helianthus annuus* (after NAWASCHIN). *B*. The male nuclei more highly magnified. *ps*, pollen-tube ; s_1, s_2, synergidæ ; sp_1, sp_2, male nuclei ; *ov*, egg-cell ; *ek*, nucleus of embryo-sac ; *a*, antipodal cells.

The physiological significance of the phenomenon of APOGAMY (11a), which has recently been accurately investigated in several Angiosperms, has already been considered (p. 302). Thorough investigation of the embryology has shown that in these cases we have to do with apogamy and not, as was first assumed, with parthenogenesis. The reduction in number of the chromosomes (p. 84) is omitted in the development of the embryo-sac, all the nuclei of which have the vegetative number of chromosomes ; they are vegetative nuclei, not generative, and the egg-cell is apogamous and not parthenogenetic. The fact that the loss of sexuality is particularly shown in polymorphic genera such as *Alchemilla*, *Hieracium*, *Taraxacum*, *Thalictrum*, is explained by STRASBURGER as resulting from the excessive mutation which has occurred; in time this, together with continuous crossing of the mutations in various directions originating from the same species, would lead to a considerable weakening of the sexuality, and from this the apogamous reproduction would follow. On the other hand there are extraordinarily polymorphic genera such as *Rosa* and *Rubus* which have only sexual reproduction. According to the most recent investigations of OSTENFELD and ROSENBERG, the genus *Hieracium* is of special interest, since the formation of the embryo within the ovule may commence in very various ways. In most a tetrad formation accompanied by a reduction division takes place, but only some of these ovules are found to have a normal embryo-sac capable of fertilisation; as a rule this is displaced by a vegetative cell which develops into an aposporous embryo-sac. In exceptional cases apogamous embryo-sacs are formed. Thus in *Hieracium* apogamy and apospory are found in addition to the normal mode of development of the embryo as a result of fertilisation. It is noteworthy that these plants of *Hieracium* in the course of generations may, after a larger or smaller number of apogamous or aposporous embryos have been produced, give rise to descendants which exhibit normal fertilisation. CLEISTOGAMY (11b) may be briefly referred to here, since GOEBEL has recently succeeded in reducing it to the same point of view. Cleistogamous flowers which frequently occur in *Impatiens*, *Lamium*, *Viola*, etc. are to be regarded as arrested formations, in which, however, the sexual organs attain maturity. They result in all cases from insufficient nutrition whether due to want of light or to an insufficient supply of mineral food materials. Since such cleistogamous flowers regularly set seed, the plants possessing them can succeed even though their normal chasmogamous flowers are often sterile. Reference may also be made to the various and often striking provisions which ensure the efficient nutrition of the embryo and endosperm. While in the simplest cases the endosperm increases greatly in size and gradually displaces the nucellus, the antipodal cells as lying next the chalaza are often specially concerned in the nutrition of the embryo-sac. In such cases they increase in number, and sometimes attain a large size. Other portions of the embryo-sac itself may grow out as long haustoria which sometimes emerge from the micropyle and sometimes penetrate into the chalazal region and the surrounding tissue; the abundant reserve materials which in some cases

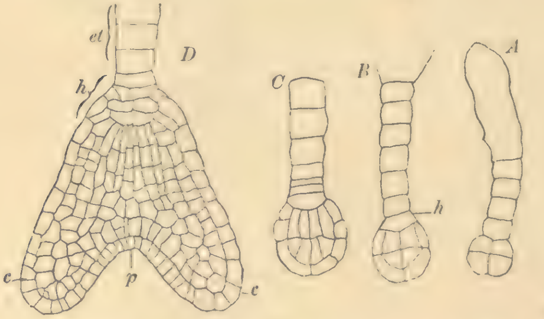


FIG. 505.—Stages in the development of the embryo of *Capsella bursa pastoris* (*A*-*D*). *h*, hypophysis; *et*, suspensor; *c*, cotyledons; *p*, plumule. (After HANSTEIN, magnified.)

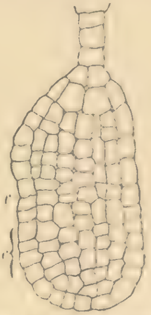


FIG. 506.—Young embryo of *Alisma Plantago*. *C*, Cotyledon; *v*, growing point (After HANSTEIN, magnified.)

(species of *Utricularia*) are accumulated beforehand, are thus made available for the nutrition of the macrospore.

The Fruit (12).—While the formation and structure of the seed presents nothing peculiar to the Angiosperms, the fruit in that group exhibits a great variety in its development and requires further consideration here.

Such a variety in the fruit might be anticipated from the range in structure of the gynaeceum described above. The product of the individual carpels associated in such apocarpous gynaecea as those of the Rosaceae will here be termed PARTIAL FRUITS or FRUITLETS, while the product of the whole gynaeceum will be spoken of as the FRUIT. The hollowed-out or projecting floral axis bearing the carpels may be included in the fruit. In the case of fruits resulting from syncarpous gynaecea the further development of the wall of the ovary as the PERICARP has to be especially considered. The outermost, middle, and innermost layers of this are distinguished as EXOCARP, MESOCARP, and ENDOCARP respectively. According to the nature of the pericarp the forms of fruit may be classified as follows:—

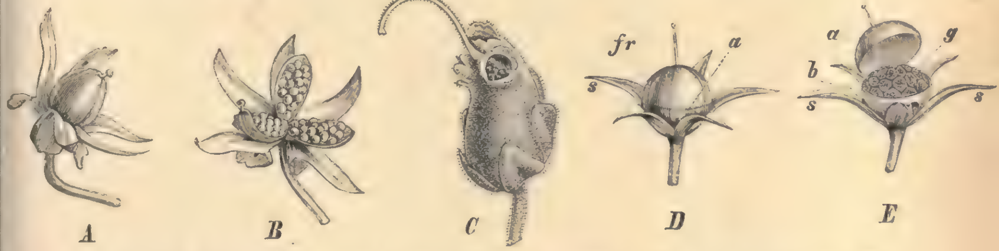


FIG. 507.—Modes of dehiscence of capsular fruits. *A*, *B*, capsule of *Viola tricolor* before and after their dehiscence; *C*, poricidal capsule of *Antirrhinum majus* (magnified); *D*, *E*, pyxidium of *Anagallis arvensis* before and after dehiscence.

1. A fruit with a dry pericarp, which opens when ripe, is termed a CAPSULE (Fig. 507). When dehiscence takes place by a separation of the carpels along their lines of union the capsule is SEPTICIDAL; when the separate loculi open by means of a longitudinal split, it is termed LOCULICIDAL, and when definite circumscribed openings are formed, it is termed PORICIDAL. As special types of frequent occurrence may be mentioned: The FOLLICLE, which is a capsule developed from a single carpel and opening by separation of the ventral suture, *e.g. Aconitum napellus* (Fig. 594): The LEGUME or pod, which differs from the follicle in dehiscing by both ventral and dorsal sutures, *e.g. Cytisus laburnum* (Fig. 642): The SILIQUA consists of two carpels and typically dehisces at maturity by their separation from a septum lying in the plane of the sutures. The

fruit of the Cruciferae, *e.g. Cheiranthus Cheiri* (Fig. 612), is of this nature. The PYXIDIUM opens by the removal of a lid, *e.g. Anagallis* (Fig. 507).

2. DRY INDEHISCENT FRUITS have a dry pericarp which does not open at maturity. Those with a hard pericarp are termed NUTS. An indehiscent fruit containing one seed, the coat of which is adherent to the leathery pericarp, is known as a CARYOPSIS (*e.g.* Grasses). When the seed is distinct from the pericarp, as in the Compositae, Polygonaceae, etc., it is termed an ACHENE (Fig. 508).

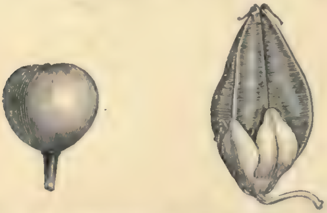


FIG. 508.—Dry indehiscent fruits. *A*. Nut of *Fumaria officinalis* (× 6). *B*. Achene of *Fagopyrum esculentum* (× 2). (After DUCHARTRE.)

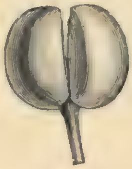


FIG. 509.—Schizocarp of *Galium mollugo*. (After DUCHARTRE, × 6.)

3. When a dry fruit, consisting of several carpels, separates at maturity into its partial fruits without the latter opening, it is termed a SCHIZOCARP (*e.g.* Umbelliferae, *Malva*, *Galium*, Fig. 509).

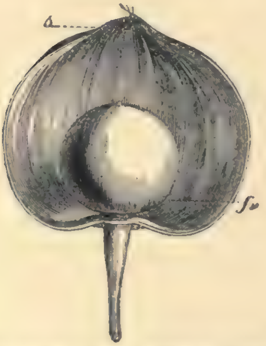


FIG. 510.—Fruit of *Physalis alkekengi*, consisting of the persistent calyx *s*, surrounding the berry *fr*, derived from the ovary. (After DUCHARTRE.)

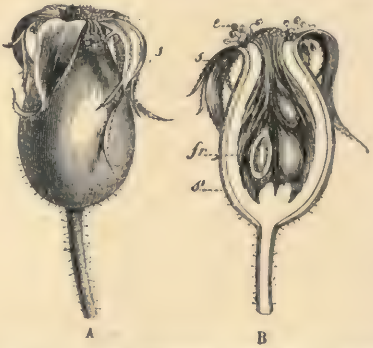


FIG. 511.—Fruit of *Rosa alba*, consisting of the fleshy hollowed axis *s'*, the persistent sepals *s*, and the carpels *fr*. The stamens *e* have withered. (After DUCHARTRE.)

4. A BERRY is a fruit in which all the layers of the pericarp become succulent, as in *Vaccinium*, *Vitis*, etc.; when at complete maturity the succulent tissue dries up a DRY BERRY results (*Capsicum*). In a few cases berries may be dehiscent, as in *Myristica* and some Cucurbitaceae.

5. In the DRUPE the pericarp is differentiated into a succulent

exocarp and a hard endocarp. *Prunus Cerasus* (Fig. 627), and *Juglans regia* (Fig. 559), are familiar examples.

Fruits which do not originate from the ovary alone are found in *Rosa* (Fig. 511), in which the succulent receptacle protects the partial fruits and still bears the calyx on its margin, and in *Physalis* (Fig. 510), the berry of which is enclosed in the greatly enlarged calyx.

When on the other hand the group of fruits borne on an inflorescence has the appearance of a single fruit the structure may be termed a SPURIOUS FRUIT. The Fig (*Ficus*) is the best-known example of this, but similar spurious fruits are especially frequent in the Urticaceae and Moraceae. The comparison of a Blackberry which is the product of a single flower with the spurious fruit of the Mulberry will show how closely the two structures may resemble one another (Fig. 512).

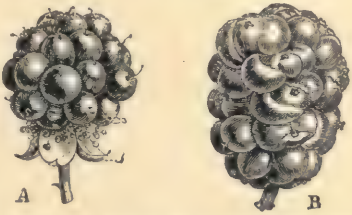


FIG. 512.—*A*, Merocarpic fruit of *Rubus fruticosus*, consisting of a number of drupes; *B*, inflorescence of Mulberry (*Morus nigra*) bearing a number of small drupes. (After DUCHARTRE.)

The above enumeration of the most important and frequently recurring forms of fruit is in no sense exhaustive. It should be added that the various forms are only to be understood when regarded from an œcological point of view. The form and other peculiarities of the fruit must be considered in relation to the distribution of the seeds. In the distribution of fruits and seeds, as in the transfer of pollen to the stigma, different means of transport, especially wind, water, and animals, are made use of by plants. (Cf. the account in the physiological section, p. 318.)

SUB-CLASS I

Monocotylae (13)

The Monocotyledons, or Angiosperms which possess a single cotyledon, are in general habit mostly herbaceous, less frequently shrubs or trees.

In germination the radicle and hypocotyl of the small embryo emerge from the seed-coat, while the sheath-like cotyledon usually remains with its upper end within the seed and absorbs the materials stored in the endosperm, which is usually well developed. The growth of the main root is sooner or later arrested and its place taken by numerous adventitious roots springing from the stem. In the Grasses these are already present in the embryo within the seed. Thus a single root system derived by the branching of a main root, such as the Gymnosperms and Dicotyledons possess, is wanting throughout the Monocotyledons.

The growing point of the stem remains for a longer or shorter time enclosed by the sheath of the cotyledon. Later it bears in two-ranked or alternate arrangement the leaves, which have long sheaths and continue to grow for a considerable time at their bases. The growth of the stem is often limited; branching is in many cases entirely wanting, and rarely results in the development of a highly branched shoot-system. The leaves are mostly sessile and parallel-veined, and of a narrow, elongated, linear, or elliptical shape (Fig. 513).

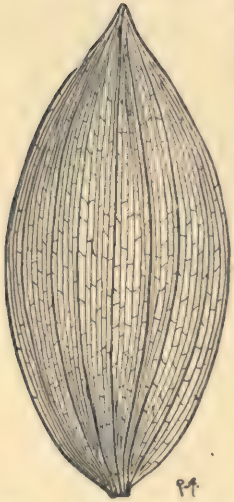


Fig. 513.—Leaf of *Polygonatum multiflorum* with parallel venation. (¾ nat. size.)

Anatomically the Monocotyledons are characterised by their closed vascular bundles in which no cambium is developed; these are uniformly scattered in the cross section of the stem (cf. Fig. 101). Secondary thickening is consequently wanting in Monocotyledons, and in the rare cases in which it is found results from the formation at the periphery of the central cylinder of additional closed bundles embedded in ground-tissue (cf. p. 144).

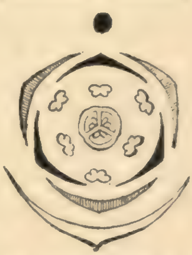


Fig. 514.—Diagram of a typical Monocotyledonous flower.

The flower in the Monocotyledons is usually pentacyclic and has two whorls constituting the perianth, an androecium of two whorls, and a gynaeceum of a single whorl. The typical number of members in each whorl is three. The two whorls of the perianth are usually similarly formed and thus constitute a perigone (Fig. 514). The floral formula of such a flower is P 3 + 3, A 3 + 3, G (3). An increased number of whorls, or of the members within a whorl, is only found in the Helobiae.

In this and in the apocarpous gynaeceum of the Helobiae an approach to the Polycarpicae, among the Dicotyledons, can be recognised, and the attempt has been made to derive the Monocotyledons from the polycarpic Dicotyledons by means of this order. This assumption is further supported by the spiral arrangement (13a) of the carpels, and apparently of the stamens also, in the genus *Sagittaria*. This possible origin of the Monocotyledons deserves more thorough investigation since no other has yet been indicated, and the Polycarpicae have formed the point of departure of a number of divergent lines of descent.

Order 1. Helobiae

Water or marsh plants with actinomorphic flowers. Gynaeceum, frequently apocarpous; carpels in two circles. Seeds, exalbuminous; embryo, large. Indehiscent fruits.

Family 1. **Alismaceae** (13b).—*Alisma Plantago*, *Sagittaria sagittifolia*, and *Butomus umbellatus* have long-stalked panicles or umbels, and occur as marsh-plants. The individual flowers have a calyx and a white (in *Butomus*, reddish) corolla. Androecium, in *Butomus* A 6+3, in *Alisma* A 6. Gynaeceum apocar-

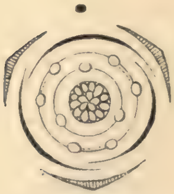


Fig. 515.—Floral diagram of *Echinodorus parvulus*, one of the Alismaceae. (After Eichler.)

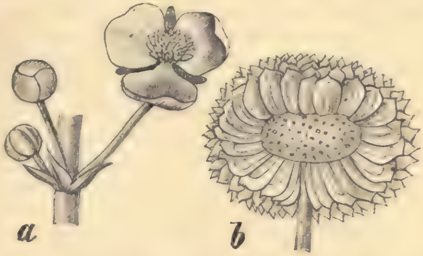


Fig. 516.—*Sagittaria sagittifolia*. *a*, Flower; *b*, fruit after removal of some of the carpels. (Magnified; *b*, after Engler and Prantl.)

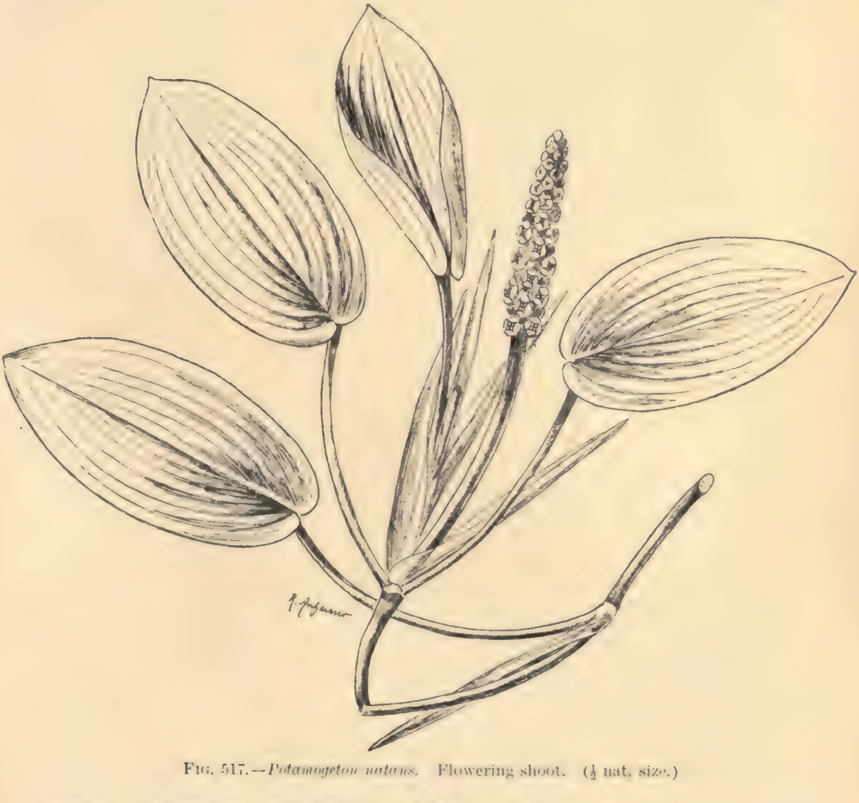


Fig. 517.—*Potamogeton natans*. Flowering shoot. (½ nat. size.)

pous, in *Butomus* G 3+3, in *Alisma* G ∞. *Sagittaria* is monœcious with flowers that by suppression of stamens or carpels are unisexual. Male flowers, with numerous stamens and sterile carpels; female flowers, with staminodes and numerous free carpels inserted on the convex floral-receptacle (Figs. 515, 516). Leaves in *Butomus*, linear, channelled, and triangular in cross-section; in *Alisma* and *Sagittaria*, long-stalked, with spoon-shaped and sagittate leaf-blades respectively. Individuals of both genera growing in deep flowing water have long ribbon-shaped leaves, similar to those that appear as a transition type in germination; such plants do not flower.

Family 2. **Juncaginaceae**.—Habit grass-like, *Triglochin*.

Family 3. **Potamogetonaceae** (Fig. 517).—Many species of *Potamogeton* are distributed over the earth in standing or flowing water. Flowers hermaphrodite, tetramerous. Gynaeceum apocarpous. Inflorescence a spike. Leaves usually submerged, with a long sheath, slit on one side, formed from the axillary stipules. *P. natans*, the common Pond-weed, at the time of flowering has usually only floating leaves, the cylindrical, submerged water-leaves having disappeared by then. *Ruppia maritima* and *Zanichellia palustris* grow in brackish water. *Zostera marina*, Grass-wrack, occurs commonly on all north temperate coasts and is used for stuffing cushions (cf. p. 307).

Family 4. **Naiadaceae**.—The single genus *Naias* contains a number of freshwater plants with diclinous flowers.

Family 5. **Hydrocharitaceae**.—*Hydrocharis morsus ranae* and *Stratiotes aloides* are floating plants occurring in Britain, which are vegetatively propagated by runners; they pass the winter at the bottom of the water, in some cases as special winter buds (cf. p. 301), and grow up again in the spring. Flowers diœcious; perianth differentiated into calyx and corolla. The male flower has several trimerous whorls of stamens; the female flower possesses staminodes and two trimerous whorls of carpels. Ovary inferior, entomophilous. *Vallisneria spiralis* (cf. p. 307). *Elodea canadensis*, the Canadian water-weed.

Order 2. Glumifloræ

This order consists entirely of annual or perennial plants of grass-like habit. A woody stem only appears in the genus *Bambusa*. The association in more or less complex inflorescences of numerous flowers, which lack a proper perianth but are enclosed by scaly bracts (glumes), is a common character of the order. The perianth is either completely wanting or reduced to a series of scales or bristles. The inner whorl of stamens is also wanting. The superior ovary is always unilocular and contains only one ovule; it is formed of three, two, or of a single carpel. The large size and feathery and papillose form of the stigmas stand in relation to the wind pollination. Fruits indehiscent.

Family 1. **Cyperaceae**.—The Sedges are characterised by their triangular stems, which are usually neither swollen at the nodes nor hollow, and by their closed leaf-sheaths. The flowers are unisexual and usually monœcious or are hermaphrodite; ovary formed of two or three carpels with an erect, basal, anatropous ovule. Pericarp not coherent with the seed-coat; embryo small surrounded by the endosperm.

The genera *Cyperus*, *Scirpus*, and *Eriophorum* have hermaphrodite flowers. Fig. 518 represents a plant of *Scirpus setaceus*, which is an annual, in flower. Leaves rigid, channelled above. Fertile shoots with the uppermost internode elongated. Spikes 1-3, terminal; enclosed by imbricating bracts and displaced to one side by the subtending bract the line of which continues that of the stem. Only the large, lowermost bracts are sterile, the others have each a naked hermaphrodite flower in their axils. Other species have the perianth represented by bristles. The Cotton-grass (*Eriophorum angustifolium*), which when flowering is inconspicuous, bears at the summit of its fertile shoots 3-7, long-stalked, erect spikelets with numerous, imbricate bracts. Around the base of each flower are numerous hairs, which are concealed by the projecting stamens and style. When the plant is in fruit the hairs, which have become about 3 cm. long, project freely from between the bracts and constitute a valuable means of dispersal for the fruits. The white colour of the hairs makes the now pendulous spikelets of the Cotton-grass a conspicuous feature of peat-moor vegetation (Fig. 519). ***Cyperus papyrus***, in Egypt and Sicily.

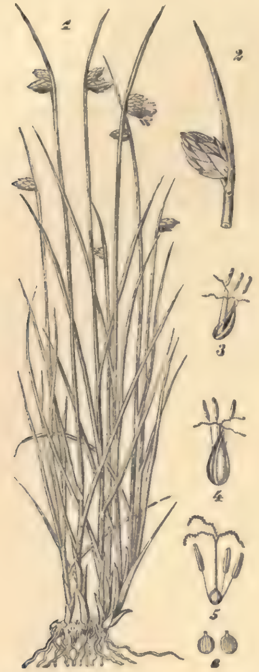


FIG. 518.—*Scirpus setaceus.* *1*, plant in flower; *2*, upper portion of a flowering shoot; *3*, single flower; *4*, the same from behind; *5*, the same without the bract; *6*, fruit. (After HOFFMANN. *1*, nat. size, the others × 2-6.)

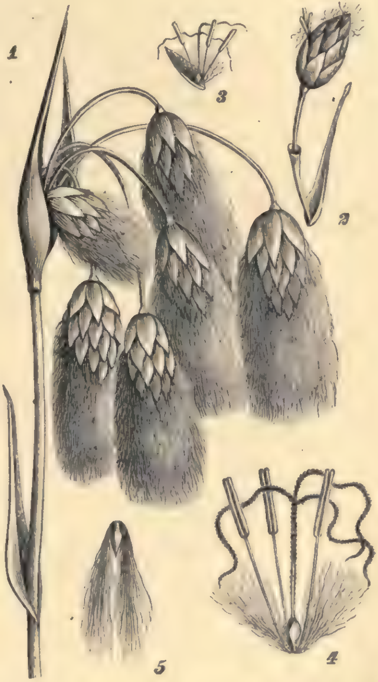


FIG. 519.—*Eriophorum angustifolium.* *1*, Inflorescence; *2*, a single spikelet; *3*, single flower; *4*, flower with bract removed; *5*, fruit. (After HOFFMANN; *1*, about nat. size; the others × 3-5.)

The genus *Carex* is for the most part monœcious, and its flowers are naked and unisexual. Male spikes simple; in the axil of each bract is a male flower formed of three stamens. The female spikes bear in the axil of each bract a secondary shoot; the axis of this is included in the tubular subtending bract (utriculus) together with the pistil (formed of 2 or 3 carpels) which is borne in the axil of the latter (Fig. 520).

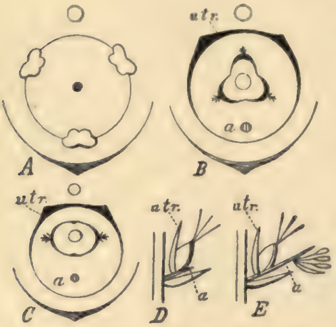


FIG. 520.—*A*, Floral diagram of a male flower of *Carex*; *B*, of a female flower with three stigmas; *C*, of a female flower with two stigmas; *D*, diagram of a female flower of *Carex*; *E*, diagram of the hermaphrodite spikelet of *Elyna*; *a*, secondary axis; *utr*, utriculus or bract of the secondary axis. (After EICHLER.)

Family 2. **Gramineae.** — The stems of the true Grasses are cylindrical, and have hollow internodes (exceptions Maize and Sugar-cane); the nodes are swollen; the leaves are two-ranked and their sheath is usually split and thickened at the node. At the junction of the sheath and leaf-blade, a membranous structure (the ligule) projects (cf. Fig. 36). The flowers of the Gramineae are grouped in spicate, racemose, or paniculate inflorescences, which are always composed of partial inflorescences, the spikelets. Usually each SPIKELET bears several flowers. At the base of the spikelet there are usually a pair of sterile bracts (GLUMAE); sometimes there is only one, or 3-4, glumes. Continuing the two-ranked arrangement of the glumes, come the fertile subtending bracts (PALEA INFERIOR) in the axil of each of which stands a flower. The subtending bracts are often awned, *i.e.* they bear terminally or springing from the dorsal surface a stiff bristle with backwardly directed hairs (the AWN). The bracteole of each flower is represented by another scale-like bract, the PALEA SUPERIOR. Above this come two small scales, the LODICULÆ, the distension of which assists in opening the flower. Lastly the axis bears the androecium consisting of a whorl of three stamens, and the ovary composed of one carpel and bearing two feathery papillose stigmas. The ovary contains an anatropous, or slightly campylotropous ovule (cf. Figs. 521-523).

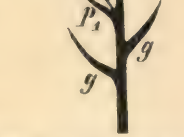


FIG. 522.—Diagrammatic representation of a Grass spikelet. *g*. The glumes; p_1 and p_2, the inferior and superior palea; *e*. lodicules; *B*, flower. The axial parts are represented as elongated.

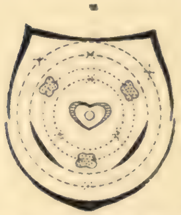


FIG. 521.—Floral diagram of the Gramineae (*Avena*) The absent members are represented by ×.

The flowers do not always show such extreme reduction; thus the flower of

Rice (Fig. 526) has a complete androecium ; that of the Bambuseae is similar and also has three lodicules, and in *Streptochæta* there is a normal monocotyledonous type of flower with all five whorls of members present (cf. the diagram in Fig. 514). The lodicules can on this evidence be regarded as corresponding to the inner whorl of the perianth. Possibly the superior palea represents two coherent leaves of the outer whorl, but proof of this is at present wanting.

The length of the staminal filaments, their attachment a little below the middle of the anthers, and the extended surface offered by the feathery stigmas are of value for wind-pollination (Fig. 523). The fruit of the Grasses is termed a caryopsis ; in it the pericarp and seed-coat are intimately united. The embryo lies in contact with the endosperm by means of its cotyledon ; this forms the SCUTELLUM and in germination serves as an absorbent organ by means of which the reserve materials in the endosperm are taken up by the seedling (Fig. 524).

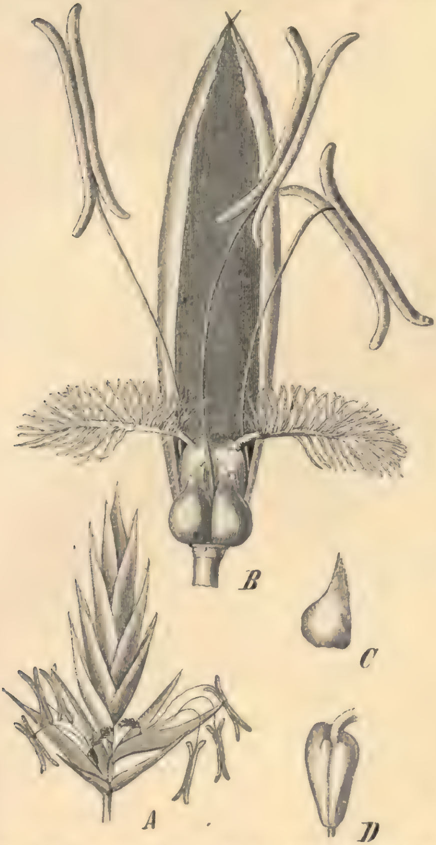


FIG. 523.—*Festuca elatior.* *A*, Spikelet (compare Fig. 522) with two open flowers below which the two sterile glumes are seen (× 3) ; *B*, Flower ; the two lodicules are in front, the superior palea behind ; the ovary bears two feathery stigmas (× 12) ; *C*, a single lodicule (× 12) ; *D*, ovary seen from the side with the stalk of one of the removed stigmas (× 12).

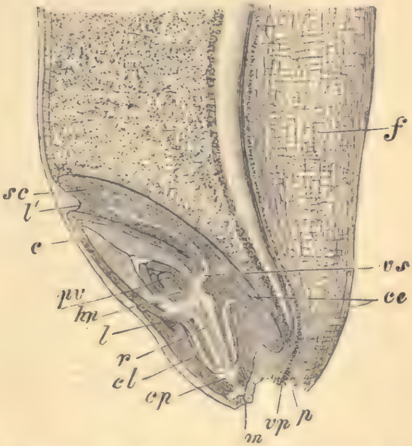


FIG. 524.—Part of median longitudinal section of a grain of Wheat, showing embryo and scutellum (*sc*) ; *vs*, vascular bundle of scutellum ; *ce*, its columnar epithelium ; *l'*, its ligule ; *c*, sheathing part of the cotyledon ; *pv*, vegetative cone of stem ; *hp*, hypocotyl ; *l*, epiblast ; *r*, radicle ; *cl*, root-sheath ; *m*, micropyle ; *p*, funiculus ; *vp*, its vascular bundle ; *f*, lateral wall of groove. (× 14.)

The most important economic plants belonging to this order are the Cereals

(Fig. 525). Wheat, *Triticum*. Spikelets single, with two or more flowers; glumes broadly ovate. KOERNICKE distinguishes as species of Wheat, 1. *Tr. vulgare*, with a number of sub-species; 2. *Tr. polonicum*; 3. *Tr. monococcum*. Rye, *Secale cereale*; Spikelets single, 2-flowered; glumes acute. Barley, *Hordeum vulgare*; Spikelets one-flowered, in groups of three; in the sub-species *H. hexastichum* and *H. tetrastichum* all the rows of spikelets are fertile, in *H. distichum* only the middle row. Oat, *Avena sativa*. Maize, *Zea mais*. The above are all cultivated in temperate climates, the Maize, largely in America, the others also in Western

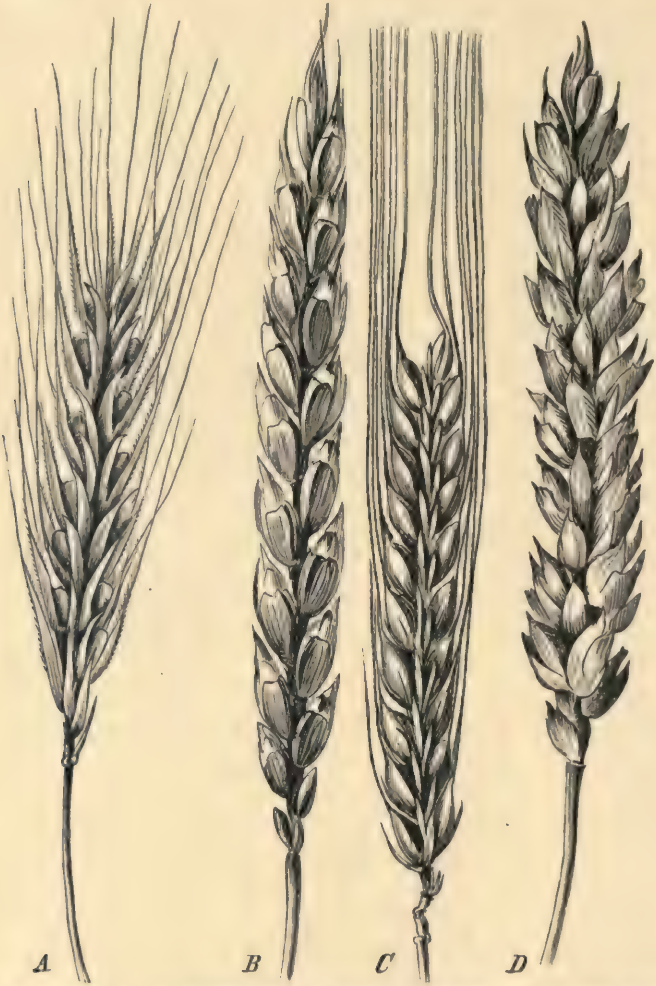


FIG. 525.—Cereals. *A*, Rye, *Secale cereale*; *B*, Spelt, *Triticum Spelta*; *C*, Two-ranked Barley, *Hordeum vulgare, distichum*; *D*, Wheat, *Triticum vulgare*.

Asia, and the south-east of Europe. In the wild state only *Triticum aegilopodioides* (from which *Tr. monococcum* is derived), *Secale montanum*, and *Hordeum spontaneum* (allied to *H. distichum*) are known. In these wild forms, the spikelets fall from the rhachis at maturity, a character that would be unsuitable in cultivated forms. The most important tropical food-plant of the order is Rice, *Oryza sativa* (Fig. 526), which is largely cultivated to the limits of the warmer temperate regions, and, when sufficient moisture is available, yields an enormous harvest. In Africa, several varieties of Millet, *Andropogon Sorghum*, are cultivated, and it forms the most important cereal for that continent. *Panicum miliaceum* and *P. italicum*, of Asiatic origin, are still cultivated, though to a diminished extent, in the Mediterranean region. The Sugar-cane, *Saccharum officinarum*, is another important food-plant; it is a perennial, growing more than six feet high, and

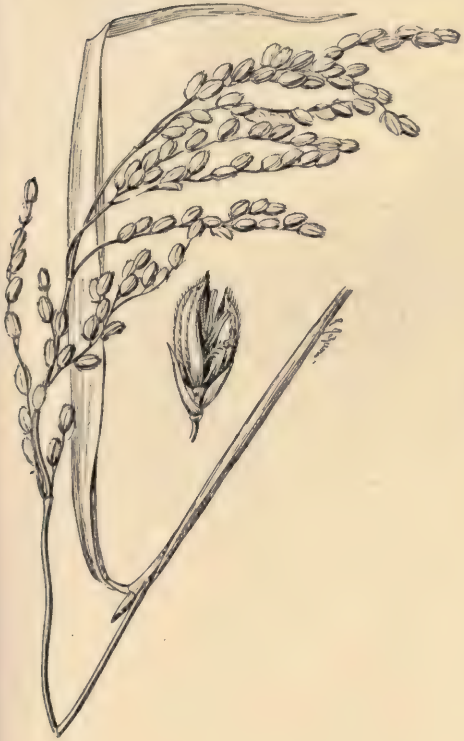


FIG. 526. — *Oryza sativa.* Panicle (½ nat. size), and a single spikelet (enlarged.) *OFFICIAL.*

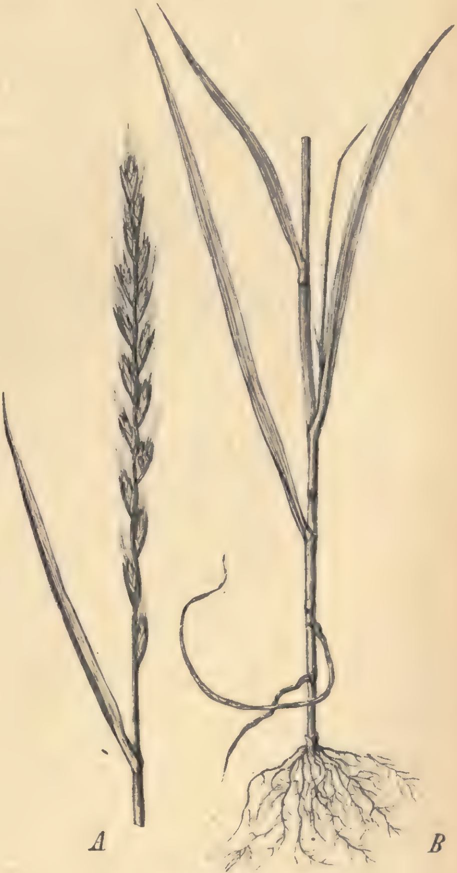


FIG. 527.—*Lolium temulentum.* *POISONOUS.*

occurs in tropical Asia. The Sugar-cane is cultivated in all tropical countries, and cane-sugar is obtained from the sap expressed from the solid stem.

Among the most important of our meadow-grasses may be mentioned *Agrostis alba*, *Alopecurus pratensis*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Avena flavescens*, *A. pubescens*, *Briza media*, *Dactylis glomerata*, *Holcus lanatus*, *Lolium perenne*, *Phleum pratense*, *Poa pratensis*, and species of *Aira*, *Bromus*, *Calamagrostis*, *Festuca*, *Melica*, etc. The tropical species of *Bambusa*, which grow to the height of trees, are utilised in many ways; from the stems are constructed houses, walls, flooring, ladders, bridges, cordage, water-vessels, cooking utensils, water-pipes, etc., and the plant is indispensable in the countries in which it occurs.

POISONOUS.—*Lolium temulentum* (Fig. 527) and *L. remotum* have poisonous fruits in relation to which fungal hyphæ occur; these plants are both annuals and can be distinguished by the absence of sterile shoots from the common *Lolium perenne* and *L. multiflorum*.

OFFICIAL.—AMYLUM (starch) is obtained from *Triticum sativum*, *Oryza sativa*, etc.; *Saccharum officinarum* provides SACCHARUM.

Order 3. Spadiciflorae

The common character of this order is afforded by the peculiar inflorescence; this is a spike with a thick, swollen, often fleshy axis and is termed a spadix. The flowers are mostly diclinous, monœcious or more rarely diœcious.

Family 1. **Typhaceae.**—Marsh plants, with long, linear leaves and long-stalked spikes, which bear a large number of flowers, the male above, the female lower down. Perianth wanting.

Family 2. **Sparganiaceae.**—Connected with the preceding family. Spikes spherical. Flowers with a perigone, but otherwise like the Typhaceae.

Family 3. **Pandanaceae.**—Trees of peculiar appearance, supported by prop-roots, or climbing, shrubby plants; all belong to the tropical countries around the Indian Ocean and to the Pacific islands. Leaves elongated, spiny, channelled above, arranged without bare internodes in three ranks on the axis. Inflorescences, ♂ or ♀, are terminal spikes in the axils of sheathing bracts. Flowers without perianth, *Pandanus* (cf. Fig. 531 in front of the Palms), *Freycinetia*.

Family 4. **Palmae.**—The Palms are an exclusively tropical and sub-tropical family, the members of which mostly attain the size of trees. Their slender stem is simple and usually of uniform diameter throughout; only the African species of *Hyphaene* have branched stems. Other forms show evident growth in thickness towards the base; this either depends on enlargement of the elements already present, or resembles the growth in thickness of arborescent Liliaceae. The leaves, which are often of gigantic size, form a terminal crown. They are either pinnately or palmately divided, the division coming about by the death of definite portions of tissue in the young leaf in

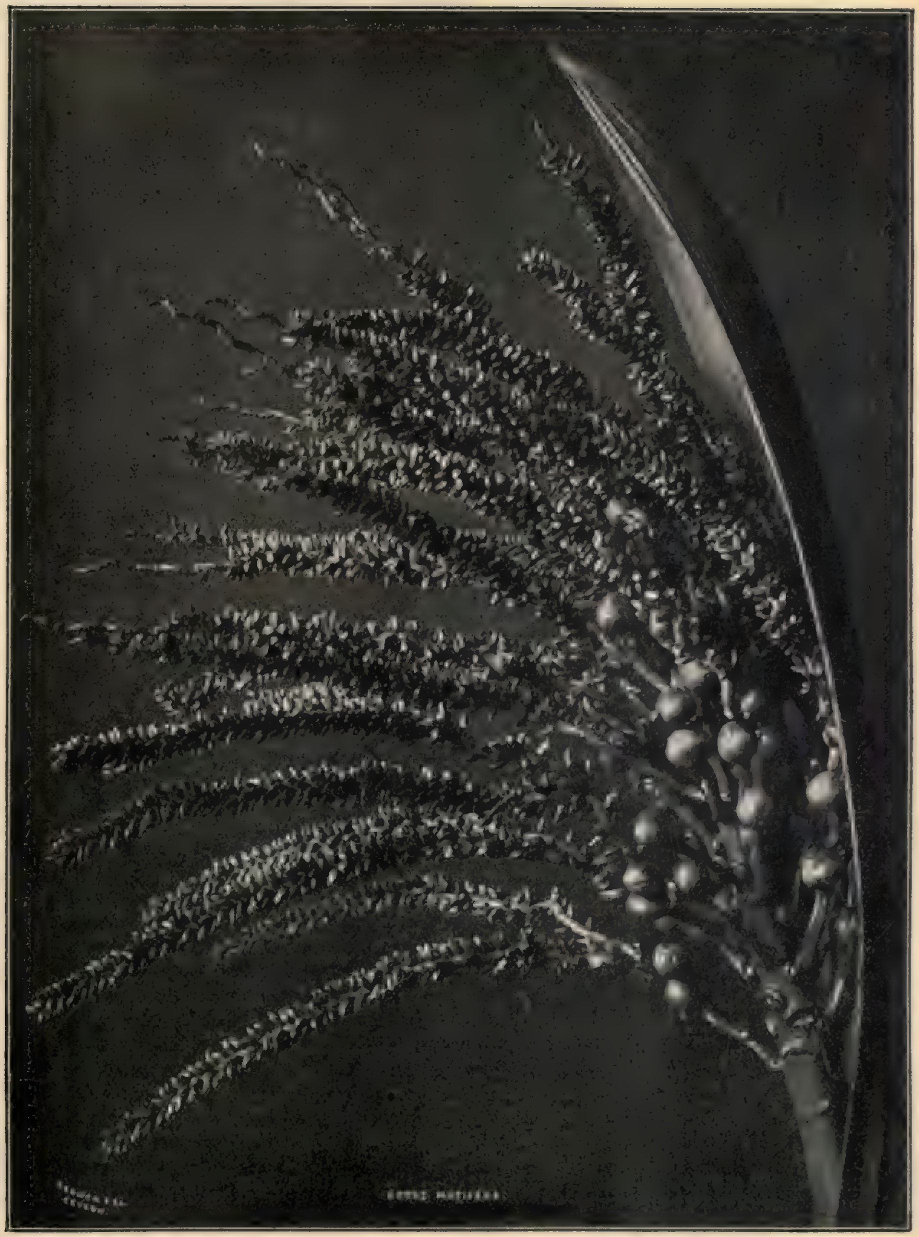


FIG. 528.—*Cocos nucifera.* Inflorescence of the Coco-nut Palm. (Greatly reduced.)

the bud. The inflorescence is in some cases terminal (*Metroxylon*), and the individual perishes with the development of the fruits. More often the inflorescences are axillary. When young, they are enclosed by a massive resistant sheath, the spathe; this bursts open and permits of the unfolding of the simple, or more usually branched, inflorescence.

The individual flowers are as a rule unisexual and constructed on the ordinary monocotyledonous type; P 3+3, A 3+3, in the male flowers, and P 3+3, G (3), in the female flowers. In *Cocos* their distribution is monœcious. Fig. 528 represents the inflorescence of *Cocos nucifera*, still partly enclosed by the spathe. The male flowers are crowded on the terminal branches of the inflorescence, while the female flowers are considerably larger and stand singly lower down. The ovary, which is here composed of three united carpels, becomes, as a rule, unilocular in the fruit, since only one carpel develops further. The ripe fruits (Fig. 529) are borne in small numbers on each inflorescence. Each consists of a coarse, fibrous exocarp, which contributes to the buoyancy of the fruit in water, and thus leads to the wide distribution of this palm on tropical coasts, and a hard endocarp on which the sutures of the three carpels can be plainly distinguished. At the base of each carpel a germinal pore is present in the endocarp (Fig. 530), but only the one in relation to which the embryo lies, remains permeable. The endosperm forms a thick layer within the endocarp; it is rich in fatty substances and produces the COPRA of commerce. The space within the endosperm is partially filled with fluid, the "milk" of the coco-nut, which is possibly of service in germination. The embryo on germination develops a massive absorbent organ which grows into the cavity of the fruit and serves to absorb the reserve materials. Fig. 531 shows the general habit of Coco-nut palms.

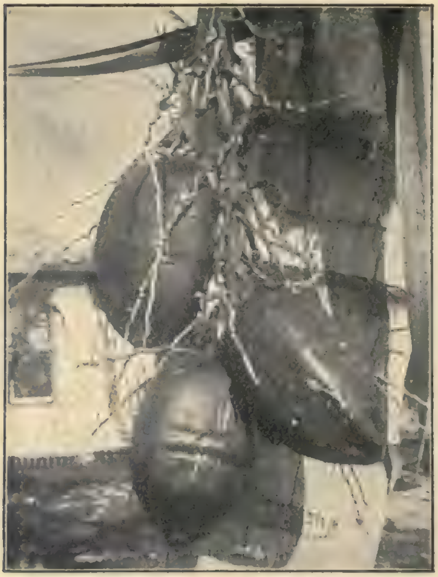


FIG. 529.—Coco-nuts on the stem.

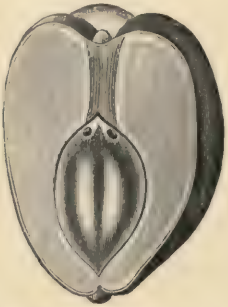


FIG. 530.—Coco-nut after partial removal of the fibrous exocarp. (After WAGNER, reduced.)

Differences are, however, found within the order. In *Areca catechu*, the fruit developed from a similar ovary to that of *Cocos* is a berry, the exocarp becoming partly fibrous and partly succulent. The white endosperm is here of stony consistence, cellulose being stored as a reserve material; the endosperm is ruminated, *i.e.* the dark seed-coat grows into it at many points and gives it a veined appearance. The fruit of the Date Palm (*Phoenix dactylifera*) is also a berry, but this arises from one of the carpels of the apocarpous gynaeceum, the other two not developing. In contrast to the other genera mentioned, *Phoenix* is diœcious. Other important economic plants among the Palms are *Elaeïs guineensis*, the African Oil Palm, species of *Calamus* which yield Malacca Cane, and species of *Metroxylon*, from which Sago is obtained; the two latter are found in the Asiatic-Australian region of the tropics. *Phytelephas macrocarpa*, an American Palm which does not form a trunk, yields vegetable ivory (the hard endosperm). Several species yield a flow of sugary sap on cutting off the inflorescence, and this is sometimes fermented to make Palm-wine, sometimes used as a source of cane-sugar (*Arenga saccharifera*).

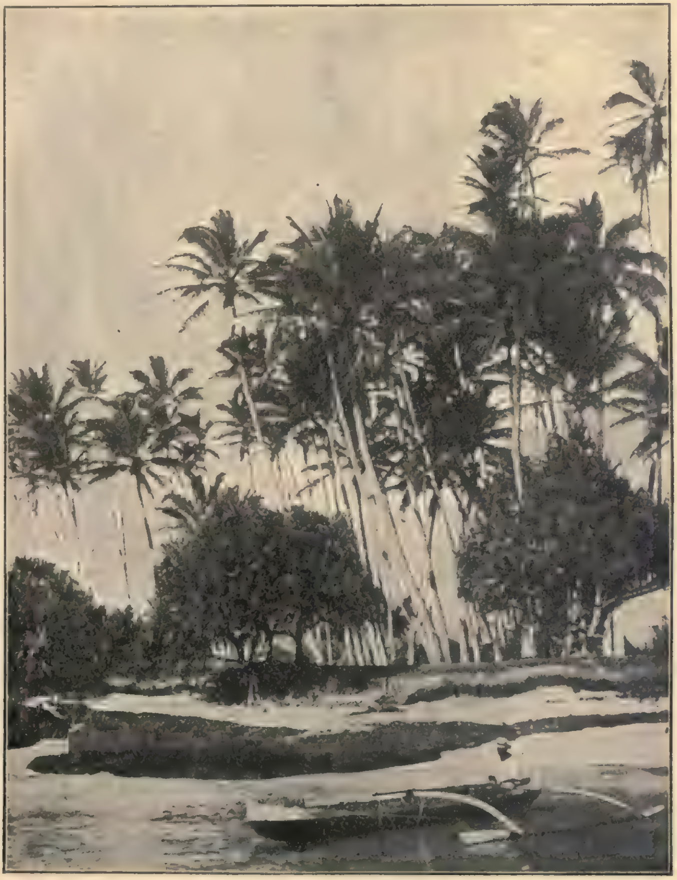


FIG. 531.—Coco-nut Palms at Hilo, Hawaii; *Pandanus odoratissimus* in front of the Palms.

Family 5. **Araceae.**—The Araceae are mostly herbs or shrubs; they take a conspicuous place as root-climbers in the damp tropical forests. The leaves of some species (*e.g. Monstera*) have the large lamina incised or perforated; this comes about by the death of definitely limited areas and is comparable to the method by which the leaves of Palms become compound. Flowers are greatly reduced, usually diclinous, borne on a swollen, fleshy axis; a spathe, often of bright colour and serving to render the inflorescence conspicuous,

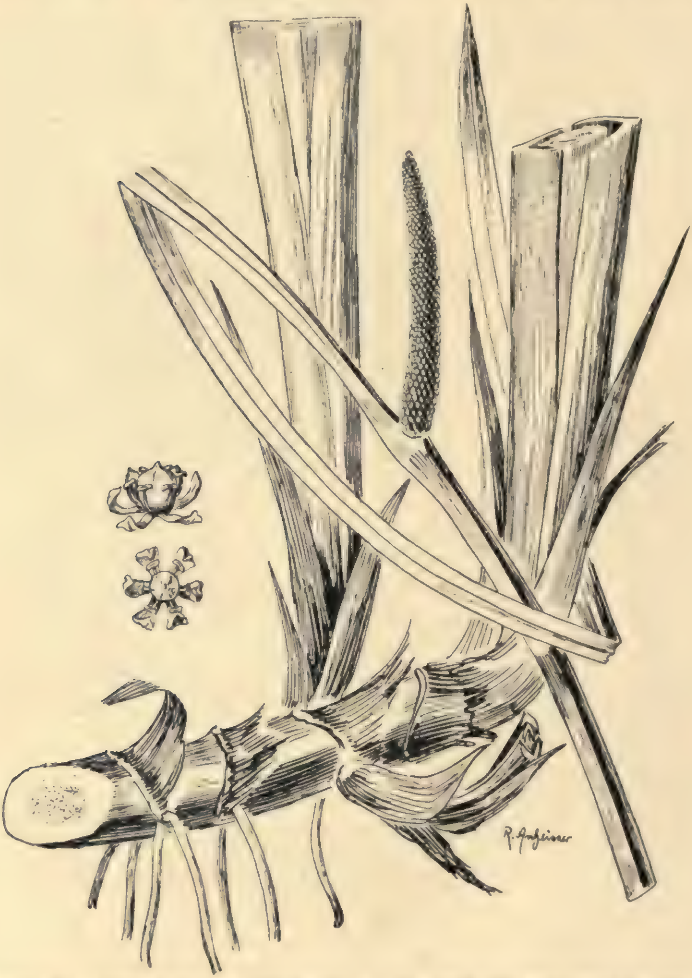


FIG. 532.—*Acorus calamus.* Flowering plant. Single flowers seen from above and from the side. (½ nat. size.)

is present at the base of the spike (*e.g.* *Anthurium scherzerianum*, *Richardia aethiopica*, both of which are commonly cultivated). Fruit usually a berry.

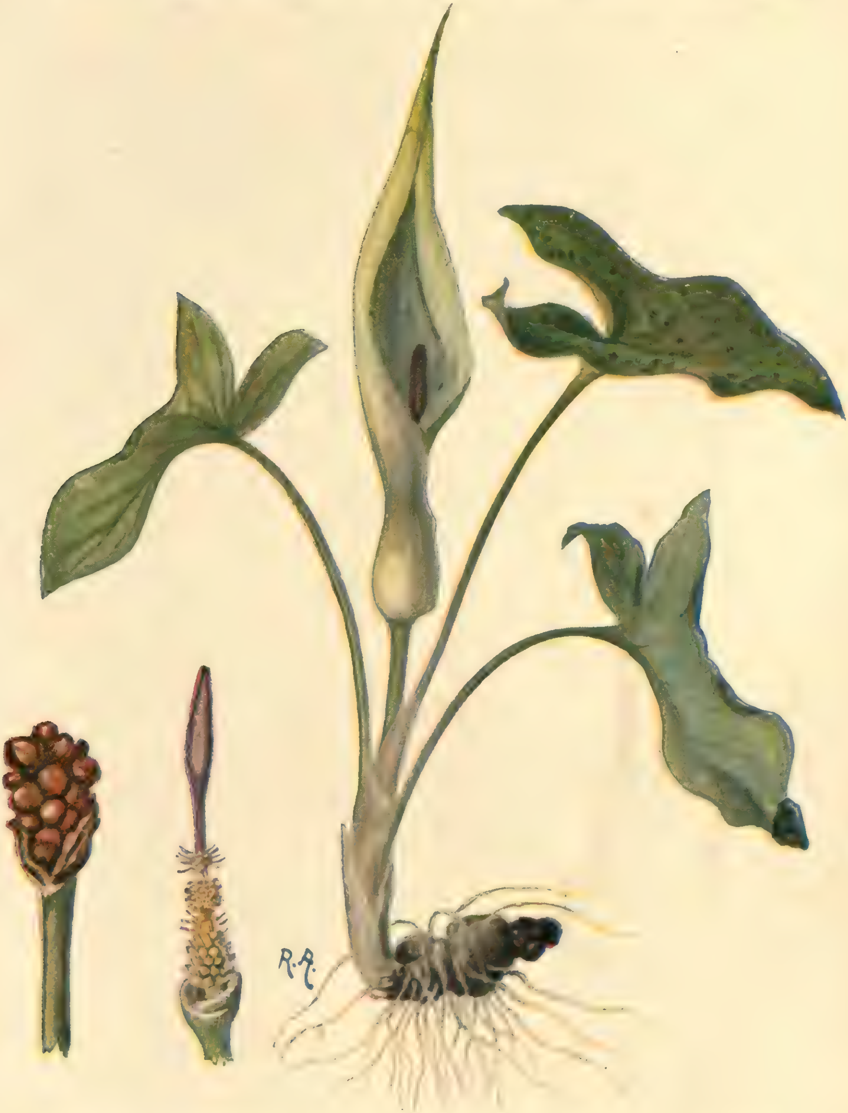


FIG. 533.—*Arum maculatum* ($\frac{1}{2}$ nat. size). Inflorescence and fruits ($\frac{2}{3}$ nat. size). *POISONOUS.*

Acorus calamus has, in the course of the last two or three centuries, spread to this country from the East. It has complete, hermaphrodite flowers; ovary trilocular. The short spadix is terminal, but is displaced to one side by the spathe which resembles the foliage leaves (Fig. 532).

POISONOUS.—Many Araceae are poisonous. *Calla palustris* in peaty swamps. *Arum maculatum* (Fig. 533), a perennial herb with tuberous rhizome, common in woods. It develops a number of stalked, hastate leaves, the brown spots on which give the plant its specific name. The flowers are monœcious, without perianth; the female flowers stand at the base of the spadix and the male a short distance above them. Above the latter come a number of sterile flowers with downwardly directed, hair-like points, which stand at the level of the constricted portion of the spathe; this is widely open above. These hairs allow insects, attracted by the peculiar scent or seeking warmth (cf. p. 244), to creep into the lower expanded portion of the spathe, but prevent their return until the female flowers have been pollinated from another individual. When this is accomplished the hairs wither and the anthers open. The escaping insects, now dusted with pollen, may enter other inflorescences and pollinate the flowers.

Family 6. **Lemnaceae.**—The Duck-weeds of our ponds and streams have naked monœcious flowers borne in depressions of the body of the plant. The flowers are surrounded by a small spathe. *Lemna, Wolffia.*

Order 4. Enantioblastae

A small order. Ovules orthotropous; embryo at summit of endosperm at opposite end from the hilum.

Family **Commelinaceae.** — Perianth developed as calyx and corolla. The hairs of the stamens afford well-known objects for the study of movements of protoplasm and nuclear divisions. Fruit a capsule. *Commelina, Tradescantia.*

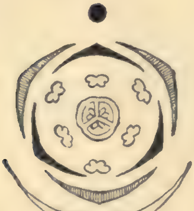


FIG. 534. – Diagram of a typical Liliaceous flower.

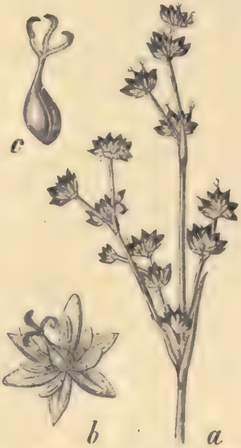


FIG. 535.—*Juncus lamprocarpus.* *a*, Part of an inflorescence; single flower (*b*) and gynaeceum (*c*) magnified.

Order 5. Liliiflorae

Flowers actinomorphic, composed of five whorls, with superior or inferior ovary. Both whorls of the perianth developed alike. Only

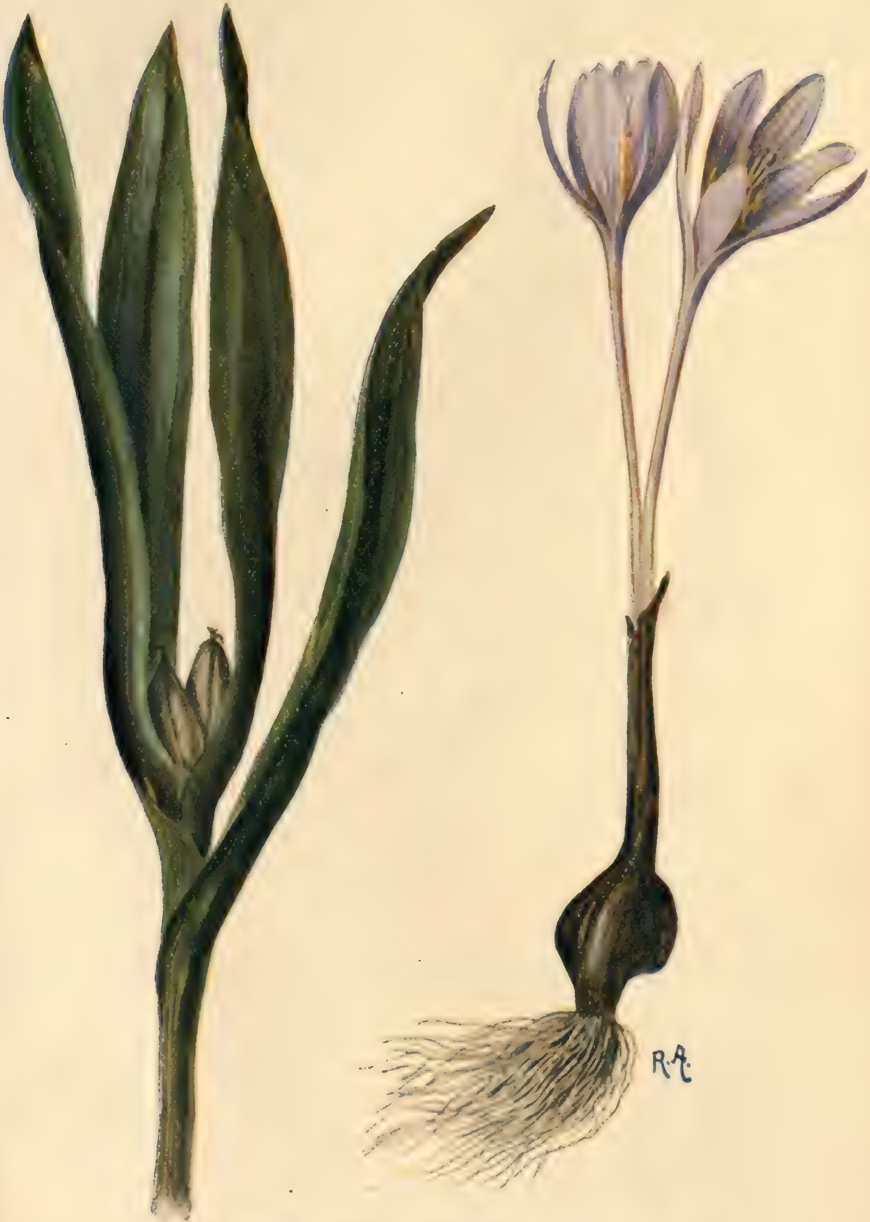


FIG. 536.—*Colchicum autumnale.* (½ nat. size.) *POISONOUS; OFFICIAL.*

in the Iridaceae is one whorl of the androecium suppressed. The gynaeceum varies in position, but it is always formed of three carpels and in most cases encloses a trilocular ovary.

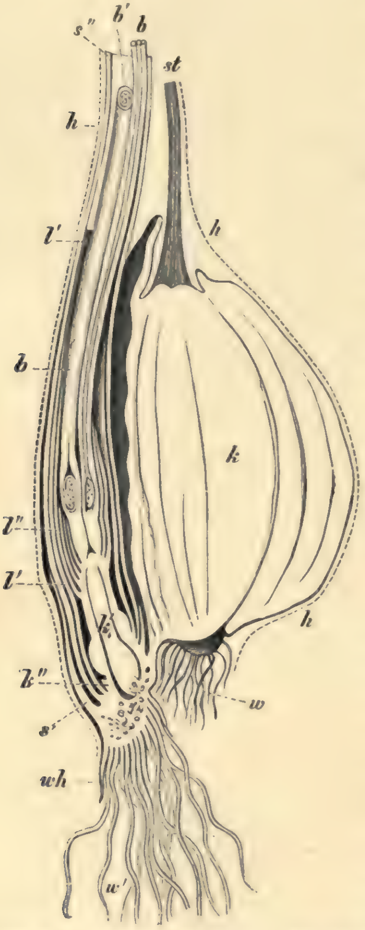


FIG. 537. — *Colchicum autumnale.* Longitudinal section through the corm of a flowering plant. Explanation in text. (After SACHS.) *OFFICIAL.*

The plants of this order show a wide range of habit. Besides herbaceous forms with bulbs or corms or subterranean rhizomes, climbing shrubs, succulent and armed, rosette-forming plants of large size and larger or smaller trees occur; the latter are restricted to tropical and sub-tropical regions.

Family 1. **Juncaceae.** — Plants of grass-like habit. Flower of complete Liliaceous type; with scaly perianth. Wind-pollination. Pollen-grains united in tetrads. Ovary superior, uni- or trilocular, bearing three, long, papillose stigmas. Endosperm floury. Fruit a capsule.

Numerous species of *Juncus* (Rush) occur in our flora, in marshy ground; the leaves are cylindrical and have large intercellular spaces. The clusters of small, anemophilous flowers (Fig. 535) are borne on the end of a shoot but are often displaced to the side by the bract which continues the line of the axis. Fruits with many seeds. *Luzula*, with flat leaves and three-seeded fruits, one of the earliest spring-flowering plants.

Family 2. **Liliaceae.**—Typical flower, with coloured, conspicuous perianth. Ovary superior. Endosperm horny or fleshy. Divided into three sub-families according to the construction of the fruit.

(*a*) Capsule with three styles; dehiscence septicidal, *i.e.* fruit splits through the septa. *Melanthieae.*

(*b*) Capsule with one style; dehiscence loculicidal, *i.e.* fruit splits opening the chambers of the ovary. *Lilieae.*

(*c*) Fruit a berry. *Asparageae.*

Colchicum autumnale, the Autumn Crocus (Figs. 536, 537), is a perennial herb growing in meadows. If a plant is examined in autumn at the time of flowering, the corm (k), to the base of which is attached the lateral shoot bearing the flowers, will be seen to be enclosed in a brown envelope (Fig. 537 h). Roots spring from the base of this lateral shoot (w'), while those of the old corm (w) are in a withered condition. At the summit of the corm the remains or scar of a dead aerial shoot will be seen (st). The lateral flowering shoot bears at its base three sheathing leaves (s', s'', l') not separated by elongated internodes. In the axil of the third of these (l') is a bud (k'') which will form the flowering shoot of the next season ; this third leaf will develop a lamina and appear above ground in spring as the first foliage leaf. A thickened internode (k') separates it from the two leaves (l'') situated higher up on the axis. Above them come the flowers (b, b'), which may be four in number, and stand in the axils of reduced leaves ; by the arrest of the growing point of the axis the flowers appear to be terminal. In spring the reserve materials from the tuber (k) are absorbed and the old tuber is pushed aside by the swollen internode (k'), which in its turn enlarges to form a new corm. The three

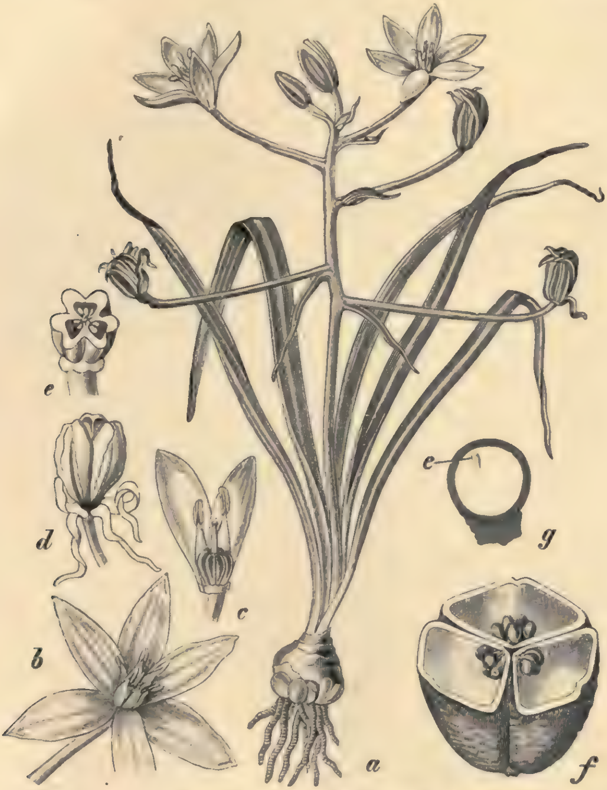


FIG. 538.—*a-e*, *Ornithogalum umbellatum* : *a*, entire plant (reduced) ; *b*, flower (nat. size) ; *c*, flower, part of perigone and androecium removed ; *d*, fruit ; *e*, fruit in transverse section. *f-g*, *Colchicum autumnale* : *f*, fruit in transverse section ; *g*, section through seed showing endosperm (*e*). (*c-g* magnified.)

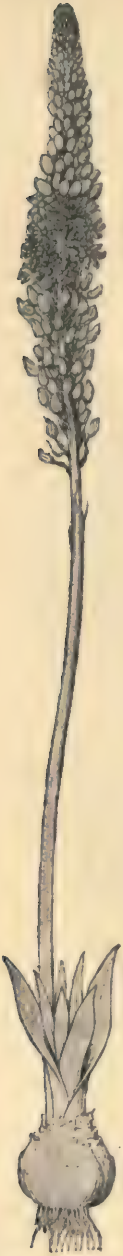


FIG. 539.—*Urginea maritima* (about $\frac{1}{10}$ nat. size.) *OFFICIAL*. (After BERG and SCHMIDT.)

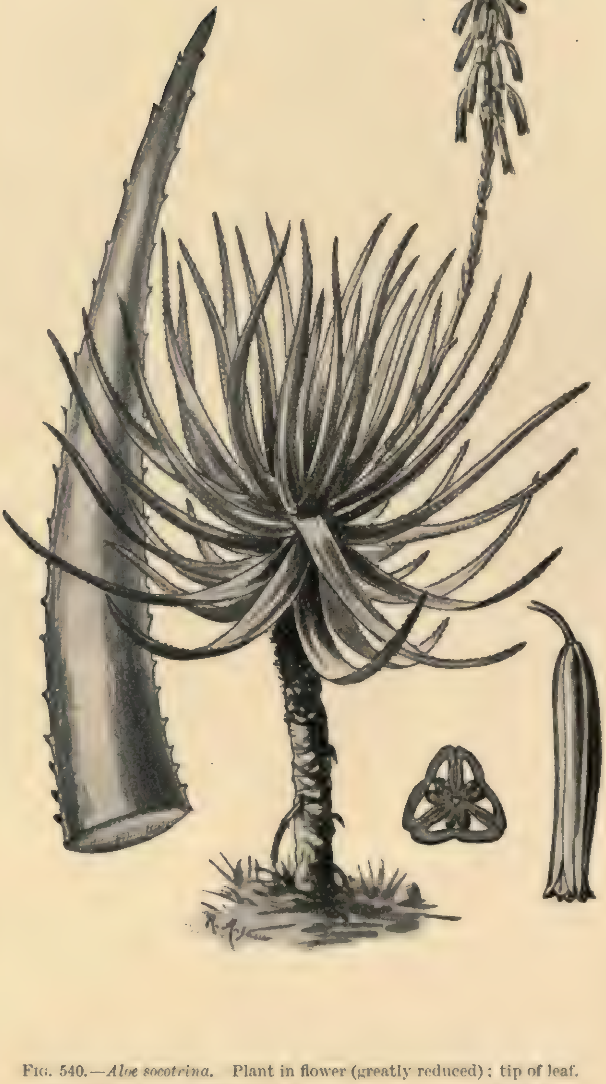


FIG. 540.—*Aloe socotrina*. Plant in flower (greatly reduced); tip of leaf, single flower, and cross-section of ovary. (½ nat. size.) *OFFICIAL*.

foliage leaves expand their long, channelled, dark green laminæ above the soil; their sheathing portions closely surround the axis. The latter bears the fruits, which contain numerous, spherical, black seeds; these are liberated by the dehiscence of the capsule at the sutures. The aerial shoot then dies, the leaf-sheaths surrounding the new corm, which bears a lateral bud (k'') in the axil of its first foliage leaf; this bud was already evident in the preceding season. *Veratrum album* is a conspicuous herb with a rosette of large, elliptical, longitudinally folded leaves. The growth of the main axis is terminated by an inflorescence, which is a panicle more than a metre in height; the leaves borne on it have long sheaths and diminish in size from below upwards. The greenish-white flowers are polygamous, *i.e.* partly hermaphrodite and partly unisexual; the ovary bears three widely-spreading styles.

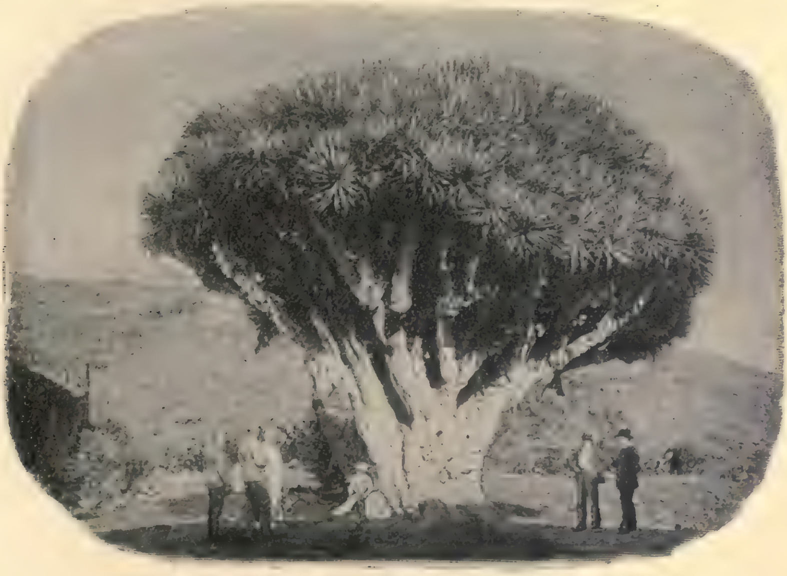


FIG. 541.—*Dracaena draco.* The dragon tree of Laguna in the Canary Islands. (From CHUN, *Aus den Tiefen des Weltmeeres.*)

Such popular flowers as *Tulipa* (Fig. 25), *Hyacinthus*, *Lilium*, *Muscari*, and *Scilla*, and vegetables as *Allium*, together with *Urginea* (Fig. 539), which occurs in the Mediterranean region, belong, on the other hand, to the Lilieae. *Ornithogalum umbellatum* (Fig. 538) will serve as an example of this group. In autumn the plant consists of a bulb, each of the fleshy scales of which has a scar at the upper end; numerous roots spring from the base of the bulb. The bulb-scales are more or less grown together. In the axil of the innermost scale is the stalk of the spent inflorescence together with a young bud bearing a number of leaves. Each of these leaves is provided with an embryonic lamina, while the continuation of the shoot is the embryonic inflorescence. In spring the leaves grow into long, linear structures, and, together with the inflorescence, appear above ground. The inflorescence is sparingly branched; the white flowers have a trilocular ovary bearing a common style. The upper parts of the leaves wither while the basal

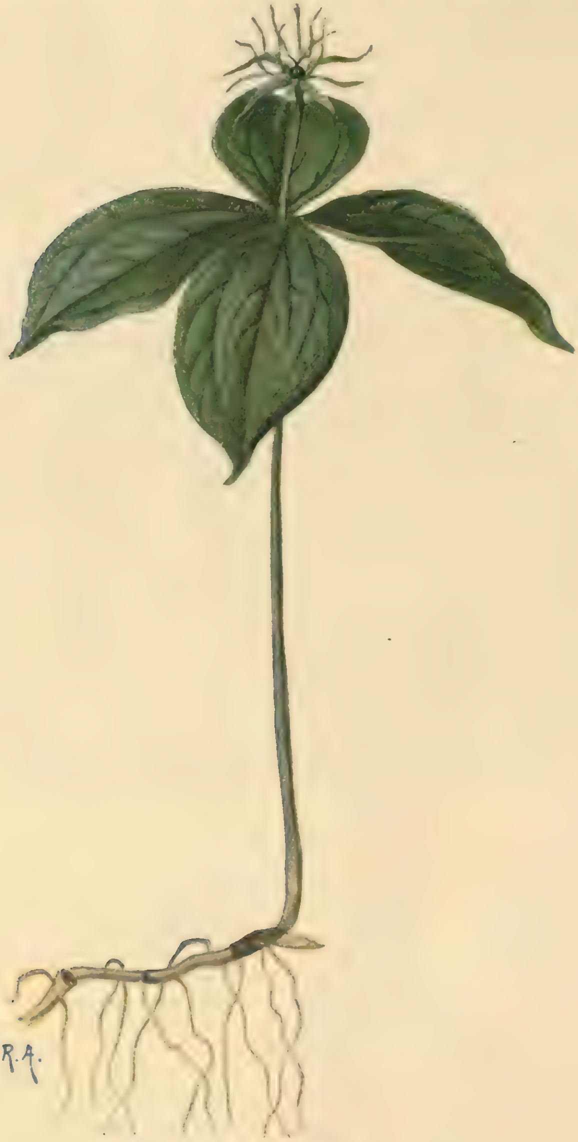


FIG. 542.—*Paris quadrifolia.* (½ nat. size.) *POISONOUS.*

portions become swollen and fleshy and stored with reserve materials; the scar at the upper part of each scale marks the place of separation of the leaf-blade. The annual course of development is essentially similar in other bulbous plants. The vegetative period is restricted to a few months, while during the cold or, in the numerous bulbous plants of warm-temperate climates, the dry seasons, the bulb is protected by its subterranean situation. *Aloe*, a genus of African plants containing many species (Fig. 540) may be mentioned as an example of an arborescent member of the Lilieae.

Dracaena (Fig. 541), an arborescent form which attains a great age and a characteristic appearance, together with the similar genera, *Cordyline* and *Yucca*, belong to the Asparageae. To the same sub-family belongs *Smilax* (Sarsaparilla), a shrubby plant of warmer countries, climbing by the help of tendril-like emergences at the base of the petioles. Other examples are *Asparagus* with bunches of phylloclades (p. 25) in place of leaves, *Convallaria* (Fig. 34), *Maianthemum*, *Polygonatum*, and *Paris quadrifolia* (Fig. 542); the latter bears whorls of four leaves, sometimes 3-6 leaves. All these plants have creeping rhizomes bearing scale-leaves; either the apex of this rhizome grows annually into the erect shoot bearing the foliage leaves and inflorescences, while the growth of the rhizome is continued by a lateral branch (*Polygonatum*, Fig. 23), or the rhizome continues its subterranean growth, the leafy shoots being developed from axillary buds (*Paris*).

POISONOUS.—Numerous Liliaceae are more or less poisonous, *e.g.* Lily of the Valley, Tulip, *Fritillaria*, *Colchicum*, *Veratrum*, *Paris*.

OFFICIAL.—*Colchicum autumnale*, seeds and corm; *Schoenocaulon* (*Sabadilla*) *officinalis*, a bulbous plant with grass-like foliage from mountains of Central America and Venezuela, seeds yield VERATRINUM. *Aloe vera*, *A. chinensis*, *A. perryi* and other species yield ALOES BARBADENSIS and ALOES SOCOTRINA. *Urginea scillae* yields SQUILL. *Smilax ornata*, etc., yield SARSAPARILLA.

Family 3. **Amaryllidaceae.**—Distinguished from Liliaceae by the inferior ovary. *Leucojum* (Fig. 543), the Snowdrop (*Galanthus*) and *Narcissus* resemble the bulbous Liliaceae in habit. *Agave*, large plants with succulent leaves from the warmer regions of America, provide fibres. *A. mexicana* provides the national drink of Mexico (pulque), obtained by fermenting the sap that flows on cutting off the inflorescence. Species of *Agave* are naturalised in the Mediterranean region but none are native there.

Family 4. **Iridaceae.**—Distinguished from Liliaceae by their inferior ovary and by the suppression of the inner whorl of the androecium (Fig. 544). The two whorls of the perianth are not always similar. Anthers extrorse. The leaves of the Iridaceae are always sessile; the underground portion is a tuberous or elongated rhizome, rarely a bulb. Capsule loculicidal.

Crocus sativus, Saffron (Fig. 545) is a plant which has long been cultivated in the East; it has a tuberous rhizome and narrow, grass-like leaves. The flowers are sterile unless pollinated with pollen of the wild form. The large stigmas furnish Saffron. Other species are cultivated as ornamental plants.

Iris, leaves overlapping in two ranks. The leaf-sheath surrounds the thick fleshy rhizome, while the sword-shaped blade stands erect and has its two surfaces alike (Fig. 546). Outer perianth segments bent downwards, inner erect. The three anthers are roofed over by the three, leaf-like styles. In *Gladiolus* the flowers are dorsiventral and the dissimilarity of the perianth leaves is more marked.

Official.—*Crocus sativus* yields saffron.

Family 5. **Dioscoreaceae.**—Climbing shrubs with diclinous flowers, sagittate or cordate, frequently net-veined leaves and large, tuberous rhizomes. Mostly tropical.

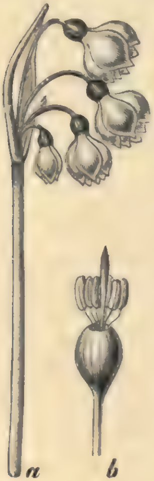
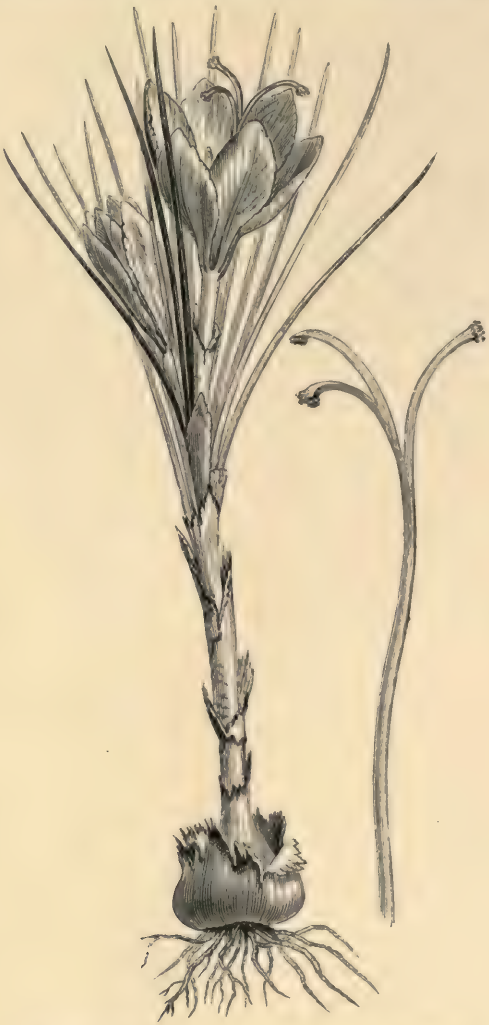


Fig. 543.—*Leucojum aestivum.* *a*, Inflorescence (reduced); *b*, gynaeceum and androecium (nat. size).



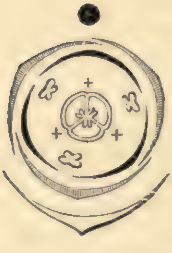


Fig. 544.—Floral diagram of the Iridaceae (*Iris*).

Fig. 545.—*Crocus sativus.* Style with tripartite stigma. *Official.* (After Baillon.)

Dioscorea batatas, Yam (China); *Testudinaria elephantipes* is often cultivated. *Tamus communis*, the Bryony, is British.

Family 6. **Bromeliaceae.**—Mostly epiphytes; flowers hermaphrodite, position

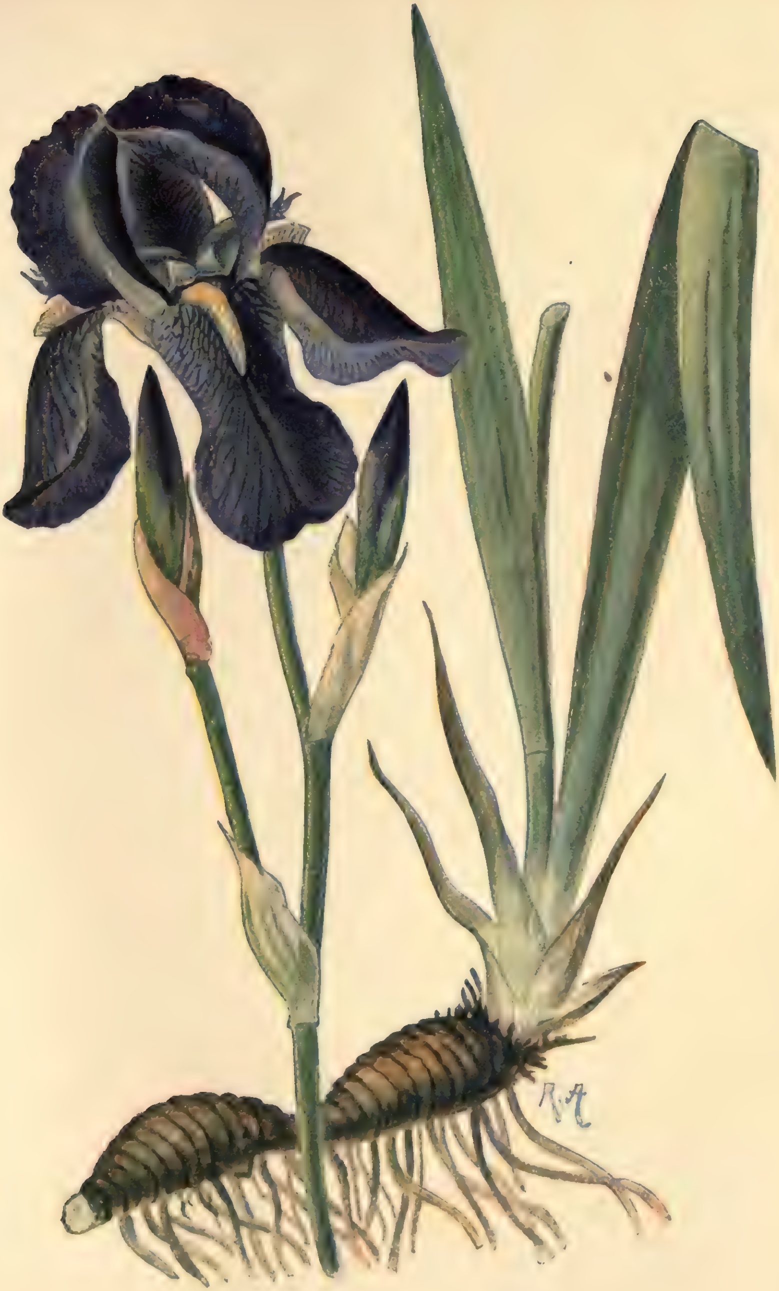


FIG. 546.—*Iris germanica.* ($\frac{1}{2}$ nat. size.)

of ovary variable. Limited to tropical and sub-tropical parts of America. The leaves are in rosettes and are typically xerophytic; in the forms which grow in the soil they are spiny. *Ananassa sativa* is cultivated and has spread in the wild state in the tropics; its inflorescence forms the Pineapple.

Order 6. Scitamineae

Tropical plants, sometimes of large size, in a few cases arborescent. Flowers dorsiventral or asymmetrical. Perianth differentiated into calyx and corolla. Androecium greatly reduced; some of the stamens represented by staminodes, and resembling the segments of the corolla. Ovary inferior, trilocular. Seeds with perisperm.

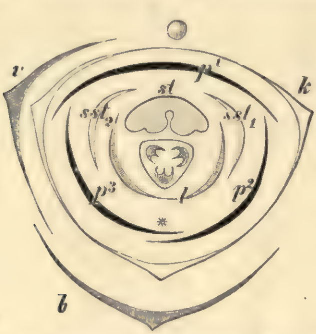


FIG. 547.—Floral diagram of Zingiberaceae (after EICHLER). *b*, Bract; *v*, bracteole; *k*, calyx; p^{1-3}, segments of corolla; sst_1, sst_2, staminodes of the outer whorl of the androecium; * the suppressed stamen of this whorl; *st*, the single fertile stamen; *l*, petaloid staminodes of the inner whorl of the androecium forming what is known as the labellum.

Family 1. **Musaceae.**—The Banana (*Musa*) is one of the most important plants of all tropical countries. The apparent, erect stem is formed of the closely overlapping, sheathing bases of the large leaves. Inflorescence, terminal. Fruit, a berry. *M. textilis* yields Manilla Hemp.

Family 2. **Zingiberaceae.**—Flowers in spikes, which in some cases resemble capitula. Flower dorsiventral. Calyx inconspicuous, tubular. Corolla with three lobes. Outer whorl of the androecium is wanting or represented by two lateral staminodes (Fig. 547, sst_1, sst_2). Only the posterior stamen of the inner whorl (*st*) is fertile; the two others are joined to form the brightly coloured, petaloid labellum (*l*). The style lies in the tubular groove between the two thecæ of the stamen. Fruit a capsule. Most plants of the family belong to tropical Asia.

Zingiber officinale, the Ginger, is an ancient cultivated plant of Southern Asia, now cultivated throughout the tropics (Fig. 548). The flattened branched rhizome is in contact with the soil by its narrow side. Leaves, two-ranked; main shoot continued by the growth of axillary buds of the lower surface. The leafy shoots, in spite of their length, are composed of the sheaths of the large, simple, entire leaves, the axis remaining extremely short. Bracts large and, especially at their margins, brightly coloured. Flowers, bright yellow, with a conspicuous, violet and spotted labellum. *Elettaria Cardamomum* and *Curcuma* have the stalks bearing their inflorescences similarly composed of leaf-sheaths. *Alpinia* and *Hedychium*, the latter of which is often cultivated, have on the other hand normal, leafy shoots bearing the terminal inflorescence.

OFFICIAL.—*Zingiber officinale*, rhizome yields GINGER. *Elettaria Cardamomum* yields CARDAMOM SEEDS.

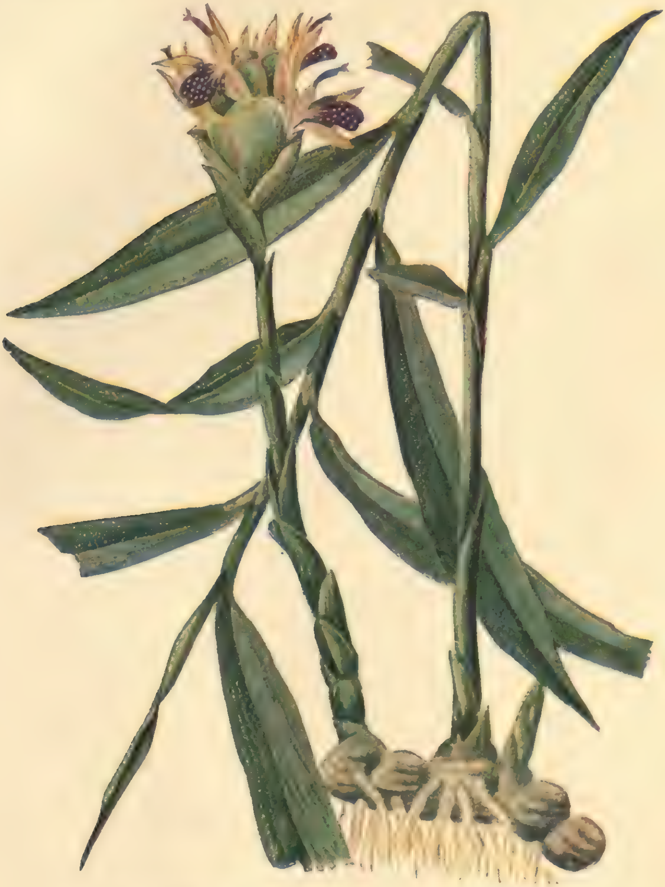


FIG. 548.—*Zingiber officinale*. (½ nat. size. After BERG and SCHMIDT.)

Family 3. **Cannaceae**.—Large-leaved herbs; often in cultivation. Flowers asymmetrical (Fig. 549). Only one half stamen fertile (*i.e.* anther with only one theca) the other half being petaloid.

Family 4. **Marantaceae**.—Large-leaved herbs. Leaves with pulvinus at junction of stalk and lamina. Stamen as in preceding order. Arrowroot is obtained from *Maranta arundinacea*.

Order 7. Gynandrae

Family **Orchidaceae.**—Perennial, herbaceous plants growing as epiphytes or in the ground, with hermaphrodite, zygomorphic flowers. Perianth petaloid, the posterior segment of the inner whorl developed as a lip or labellum, which frequently bears a spur. (The "labellum" of the Scitamineae being formed of two staminodes, is entirely different morphologically.) Androecium formed of the three anterior stamens only; the middle stamen, belonging to the outer whorl, is fertile; the other two are represented by staminodes. *Cypripedium* has these two lateral stamens of the inner whorl fertile. Gynaeceum formed of three carpels, syncarpous; ovary inferior, unilocular. Fruit, a capsule. Seeds extremely numerous, borne on parietal

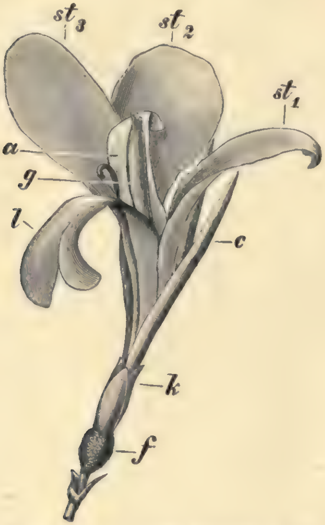


FIG. 549.—Flower of *Canna iridiflora*. *f*, Ovary; *k*, calyx; *c*, corolla; *l*, labellum; st_{1-3}, the other staminodia; *a*, fertile stamen; *g* style. (½ nat. size.)

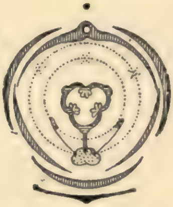


FIG. 550.—Orchidaceae. Floral diagram (*Orchis*).

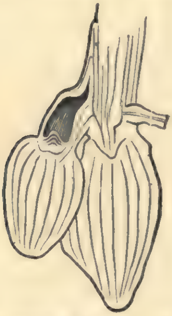


FIG. 551.—*Orchis militaris.* Longitudinal section passing through the old and new tubers. (After LUERSSEN.)

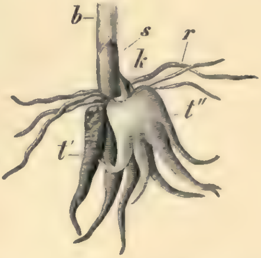


FIG. 552.—Root-system of *Orchis latifolia*. *b*, Base of stem; *s*, cataphyllary leaf; *t'*, old, *t''*, young tubers; *k*, bud; *r*, roots.

placentas (Fig. 550). The fertile stamen is adherent to the style and forms with it the COLUMN or GYNOSTEMIUM; this projects more or less in the centre of the flower. The labellum, which serves as an alighting place for visiting insects, becomes anterior either by the torsion of the whole flower through 180° (cf. Figs. 550 and 553) or by the flower being bent backwards.

This order of 6000-10,000 species is primarily divided into *Monandrae* and *Diandrae* in which one stamen of the outer whorl or two stamens of the inner whorl are fertile respectively.

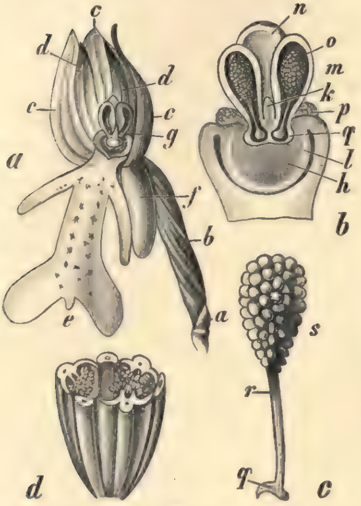


FIG. 553.—*Orchis militaris.* **a**, Flower: *a*, bract; *b*, ovary; *c*, the outer, and *d*, the two anterior inner perigone leaves; *e*, labellum with the spur *f*; *g*, gynostemium. **b**, Flower after removal of all of the perigone leaves with exception of the upper part of the labellum: *h*, stigma; *l*, rostellum; *k*, tooth-like prolongation of the rostellum; *m*, anther; *n*, connective; *o*, pollinium; *q*, viscid disc; *p*, staminodium. **c**, A pollinium: *r*, caudicle; *s*, pollen. **d**, Ovary in transverse section. (After BERG and SCHMIDT.)

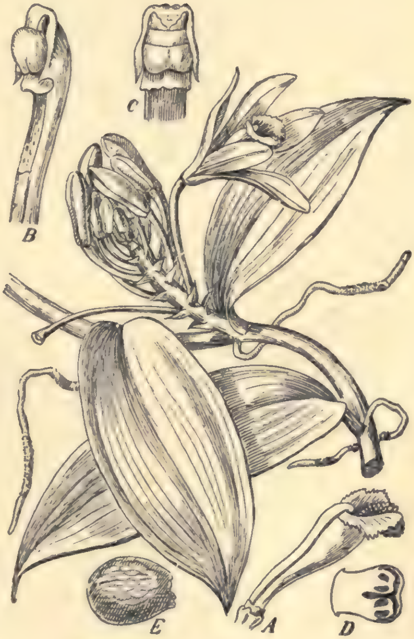


FIG. 554.—*Vanilla planifolia* (reduced. After BERG and SCHMIDT; from ENGLER and PRANTL.) *A*, Labellum and gynostemium; *B*, gynostemium from the side; *C*, summit of the gynostemium from in front; *D*, anther; *E*, seed. (Magnified.)

EXAMPLES OF BRITISH GENERA:—1. Monandrae: *Orchis*, *Ophrys*, *Gymnadenia* with tubers; *Epipactis*, *Cephalanthera*, *Listera* with branched rhizomes; *Neottia*, the Bird's-nest Orchid, *Epipogon*, *Corallorhiza*, saprophytic and almost destitute of chlorophyll. 2. Diandrae: *Cypripedium*, Ladies' Slipper.

Orchis militaris which is represented in Fig. 555 will serve as an example for more detailed consideration. At the period of flowering a pair of fleshy tubers will be found at the base of the plant, both of which are covered with root hairs. The large or brown tuber of more spongy texture continues above into the stem

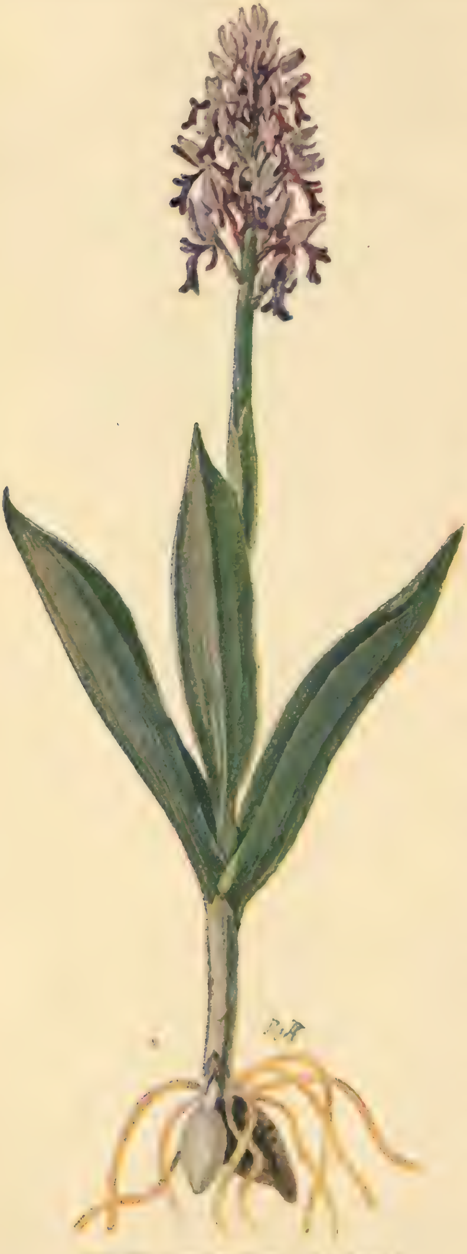


FIG. 555.—*Orchis militaris*. (½ nat. size.)

which terminates in the pyramidal inflorescence ; this axis is surrounded at the base by a pair of scale - leaves and the sheaths of the 2-4 elongated, elliptical foliage leaves. The smaller tuber is of firmer consistence and of a white colour ; it bears, as is shown in the longitudinal section (Fig. 551), a bud on its summit which already shows a pair of scale leaves. This tuber has arisen as an axillary bud in relation to one of the first scale-leaves of the plant, and with its tuberous, swollen, first root has broken through the subtending scale-leaf (Fig. 555). It is destined to replace the parent plant in the succeeding season. The anatomical and morphological differences between the tuber and the ordinary roots of the plant may be explained by the consideration that the tuber arises from several coherent roots. The existence in other species (Fig. 552) of palmately branched tubers increases the probability of this explanation.

In considering the flower, the spiral torsion of the ovary, which brings the labellum into the anterior position, must first be recognised. The labellum is tripartite and the larger middle segment is bifid at its free end. At the base of the labellum a spur is formed by the bulging out of this segment of the perianth ; this serves as the nectary, and the opening leading into it is situated just below the gynostemium (Fig. 553 *A*, *B*). The latter bears on the side that is turned towards the lower lip, and to an insect alighting on this, the large stigmatic surface (*h*) corresponding to two confluent stigmatic lobes. The third stigmatic lobe is transformed into a structure termed the rostellum (*l*, *k*) and stands in relation to the male organ. The single fertile anther consists of two thecæ joined together by the connective which appears as the end of the gynostemium. The whole mass of pollen of each of the two pollen-sacs is joined together by an interstitial substance which continues below to form a stalk ; the whole structure, which has a waxy consistence, is called a pollinium, and the stalk goes by the name of the caudicle. The caudicles terminate below in contact with the rostellum which forms tough adhesive discs. This relation to the rostellum serves to keep the pollinia, which lie free in the pollen-sacs, in position, and the adhesive discs attach the pollinia to any body that comes in contact with them. If an insect alights on the lower lip and attempts to reach the nectar secreted in the spur, its head or tongue must touch the rostellum and the pollinia will become attached to it. As the adhesive discs dry they cause the pollinia to bend forward, so that when the insect visits a second flower they will be brought in contact with the stigmatic surfaces.

All Orchids are similarly adapted to insect visitors, though in many the contrivances are far more complicated ; pollination does not take place in the absence of the insects. It should be mentioned that in some forms, *e.g. Vanilla*, the pollen remains powdery. Many tropical Orchids are cultivated in greenhouses on account of the beauty of their flowers.

SUB-CLASS II

Dicotylae (14)

The Dicotyledons with few exceptions possess a pair of seed-leaves ; these on germination either expand as green assimilating leaves or remain within the seed-coat and supply the seedling with the reserve materials stored in their cells. The growing point of the stem, lying between the cotyledons, grows into the shoot of the seedling. The main root of the embryo has meanwhile penetrated into the soil ; as a rule it persists as a tap-root and gives rise to a regularly branched root-system.

The stem has a circle of open vascular bundles, while the root on transverse section shows a regularly alternating arrangement of the xylem- and phloem-groups. The primary meristem situated in the vascular bundles of the stem, or to the inner side of the phloem in the root soon becomes completed across the medullary rays and forms a complete, meristematic ring. By means of this cambium a regular growth in thickness of the stem and root takes place (cf. Figs. 123-124, pp. 112, 114 ; Fig. 128, p. 118 ; Fig. 138, p. 129 ; Figs. 146-154, pp. 138-144).

The typical form of leaf found among Dicotyledons is provided with a longer or shorter petiole, and often has a pair of stipules developed from the leaf-base ; a leaf-sheath is usually absent. The lamina may be simple or compound ; the latter condition is always the result of branching during the development of the leaf. The margin of the leaf presents considerable variety. The venation is as a rule reticulate (Fig. 556).

The flowers of Dicotyledons exhibit a wide range in their appearance and construction. Most frequently they can be derived from a type with five whorls of five members; increase and decrease of the number both of the whorls and the members are met with. The Dicotyledons are divided into the two series of the *Choripetalae* (with free perianth segments) and the *Sympetalae* (with the petals coherent).

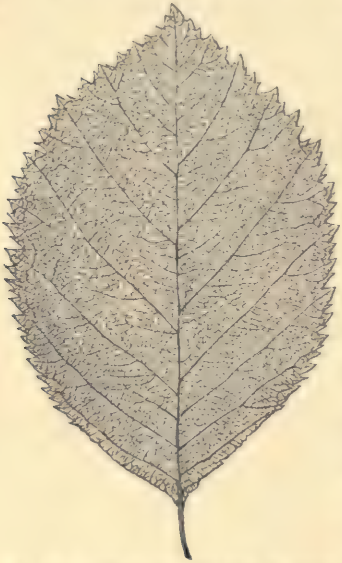


Fig. 556.—Leaf of *Crataegus* with reticulate venation. ($\frac{3}{4}$ nat. size.)

The classification adopted here corresponds in the main to that in Engler and Prantl's *Natürlichen Pflanzen-familien*, but the grouping together of a number of families under the older ordinal names has been retained.

A number of questions raised by Hallier in his recent work on the natural (phylogenetic) system of classification of flowering plants deserve consideration. For instance the separation of *Choripetalae* and *Sympetalae*, which Hallier abandons, is doubtless artificial and not altogether satisfactory. The recognition of the catkin-bearing forms as reduced and the derivation of the Dicotyledons from forms like the Magnoliaceae has much in its favour. The derivation of the Monocotyledons from the Polycarpicae is supported on quite different grounds by E. Sargant. While systematic Botany must endeavour to attain new points of view and never to regard the prevailing classification as a sort of *noli me tangere*, further developmental studies are necessary before a thorough revision of the present system can be contemplated. An investigation by Strasburger into the ovule and the formation of the endosperm in *Drimys Winteri*, a plant which in the structure of its wood recalls the Gymnosperms, has yielded no indication that the gap existing between Gymnosperms and Angiosperms can be bridged by the study of existing forms.

Series I. Choripetalae (15)

Order 1. Piperinae

The single Family of the **Piperaceae** contains a few tropical genera. Flowers as a rule unisexual and without perianth, associated in spikes; typically trimerous but usually reduced. Ovary unilocular, ovule solitary, basal and atropous. Fruit drupe-like. The embryo is

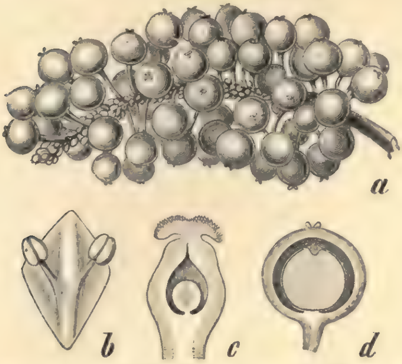


FIG. 557.—*Piper cubeba.* *a*, Infructescence; *b*, a male flower; *c*, a female flower in longitudinal section; *d*, fruit in longitudinal section. *OFFICIAL.* (After BERG and SCHMIDT.)

embedded in a small endosperm surrounded by a well-developed perisperm.

The genus *Piper* includes a large number of shrubby plants of primæval forests. *Piper nigrum*, from which the Peppers are derived, is the most important representative. This is a root-climber, native to the Malayan region, but now cultivated throughout the tropics (Fig. 558). The unripe fruits provide black pepper, while white pepper is obtained from the ripe fruits after removal of the outer layers of the pericarp. The genus *Peperomia* has hermaphrodite flowers.

OFFICIAL. — *Piper nigrum* and

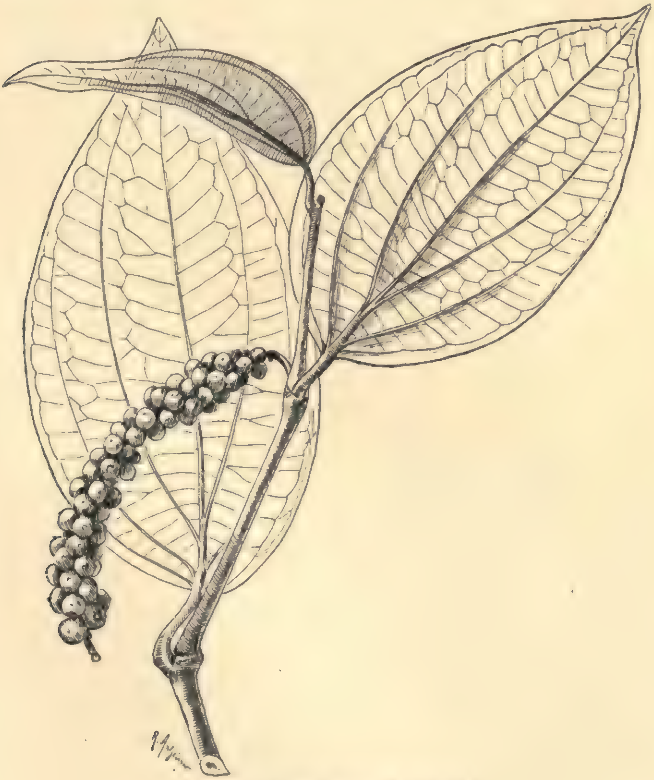


FIG. 558.—*Piper nigrum.* (½ nat. size.)

Piper cubeba (Fig. 557). The latter is a native of Java and is distinguished by the stalk-like base of the fruit from that of the Black Pepper. It provides CUBEBAE FRUCTUS.

Order 2. Juglandiflorae

Aromatic woody plants, with anemophilous, unisexual flowers in catkinate spikes, sometimes containing very few flowers. Ovary bicarpellary and unilocular with a single, basal, erect, atropous ovule. Fruit, a drupe. Seed without endosperm.

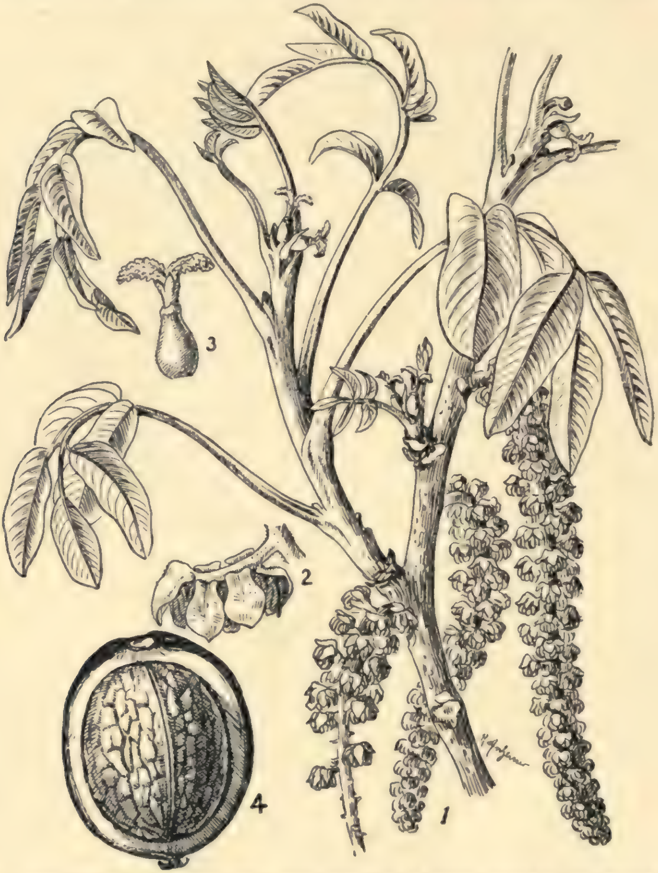


FIG. 559.—*Juglans regia.* *1*, Branch with young leaves, male catkins and at the tip female flowers. *2*, male flower. *3*, Female flower. *4*, Fruit with the outer layer of the pericarp in part removed. (½ nat. size.)

Family 1. **Juglandaceae** (15a).—Conspicuous, monœcious trees of the northern hemisphere with imparipinnate, aromatic leaves arranged alternately. Stipules wanting. Male catkins springing from the leaf-axils of twigs of the preceding year; female flowers in terminal spikes containing more or less numerous flowers. Ovary inferior.

The Walnut, *Juglans regia* (Fig. 559), is the best-known representative of the family. It is endemic in Western Asia and the eastern portion of the Mediterranean region, but the tree is in cultivation throughout Europe. In spring the axillary buds of the previous season produce long, thick, pendulous catkins bearing numerous flowers. Each of the latter has 3 to 5 perianth segments, and these together with the two bracteoles are adherent to the bract and surround the numerous stamens, which face towards the tip of the inflorescence. The female flowers in smaller numbers are borne at the summit of the young shoots. The two carpels terminate in large, feathery, diverging stigmas. The perigone is adherent to the bract and bracteoles and reaches to the summit of the inferior ovary. The single loculus encloses an atropous, basal ovule. Fruit, a drupe. The exocarp contains abundant tannin. The hard endocarp is divided into two valves in the plane of the dorsal sutures of the coherent carpels, the limits of which are indicated by the partial septum at the lower part of the fruit. Within the stone is the embryo, enclosed in a thin seed-coat. The large cotyledons, which contain oil, are lobed in correspondence with the false septa that project from the inner surface of the ovary. Endosperm wanting. Other species of *Juglans* and *Carya* yield edible seeds and valuable timbers.

Family 2. **Myricaceae.**—*Myrica gale* is a diœcious shrub with entire leaves found on moors. Some American forms yield wax derived from the fruits (p. 101).

The family of the **Casuarinaceae**, the systematic position of which is doubtful, may be mentioned here. They are trees growing by the sea-shore or on mountains, and are distributed from southern Asia and Australia throughout the Polynesian islands. Chalazogamy ([11]) was first discovered by Treub in *Casuarina*.

Order 3. Saliciflorae

Family **Salicaceae.**—Trees and shrubs with simple, alternate, stipulate leaves. Flowers in diœcious catkins, usually developed before the leaves. Both male and female flowers are naked and stand in the axils of bracts. More or less developed scale-like development of the disc or floral receptacle. Ovary of two carpels, unilocular. Fruit, a capsule containing

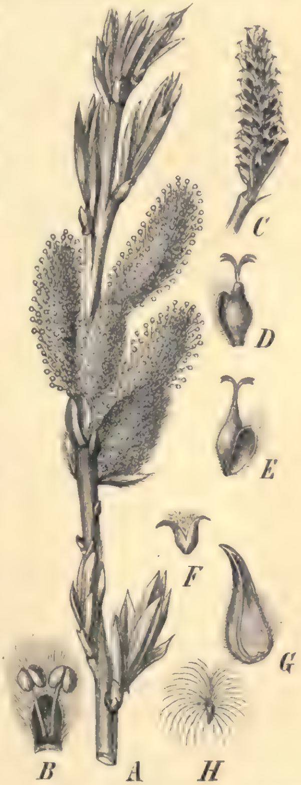


FIG. 560.—*Salix viminalis.* *A*, Flowering male twig (nat. size); *B*, male flower with subtending bract (magnified); *C*, female inflorescence; *D-E*, female flowers (magnified); *F*, fruit (nat. size); *G*, the same magnified; *H*, seed (magnified).

numerous, parietal seeds. Seeds without endosperm; seed-coat with a tuft of hairs.

This family is mainly represented in the north temperate zone. *Salix*, Willow, and *Populus*, Poplar, are the only genera. *Salix* has erect catkins and is adapted to pollination by insects; in relation to this, nectar is secreted by small scales at the base of the flower. Male flowers scented, pollen sticky. The number of stamens varies from 2 to 5 in the different species. Bracts entire (Fig. 560). Willows occur commonly by the banks of streams where their shortly stalked, narrowly lanceolate leaves give them a characteristic appearance. Some species are among the more abundant plants of high northern latitudes; they have subterranean, creeping stems, only the young shoots projecting from the soil (cf. *Salix polaris*, Fig. 198). *Populus* has anemophilous flowers; disc cup-shaped; no secretion of nectar. The long-stalked circular leaves of the Poplars give them a different habit from the Willows. Flowers similar to those of *Salix* but with divided bracts. Catkins pendulous (Fig. 561).

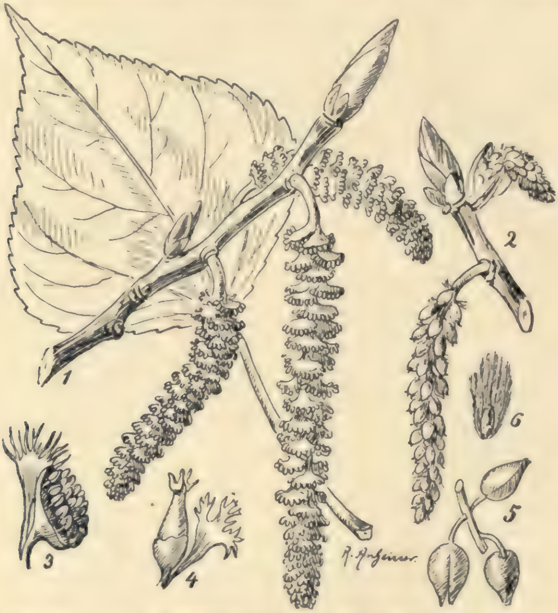


Fig. 561.—*Populus nigra*. *1*, Male inflorescence. *2*, Female inflorescence. *3*, Male flower. *4*, Female flower. *5*, Fruit. *6*, Seed. (*1*, *2*, ¾ nat. size; *3-6*, enlarged.)

Official.—Salicin is obtained from the bark of species of *Salix* and *Populus*.

Order 4. Querciflorae

Trees or shrubs usually with entire leaves and deciduous stipules. Monœcious. Male flowers in catkins. Ovary inferior; ovules pendulous. Fruit, a one-seeded nut. Endosperm wanting. Anemophilous.

This order was formerly united with the Juglandiflorae and Saliciflorae in the Amentiflorae; they include most of our important forest-trees.

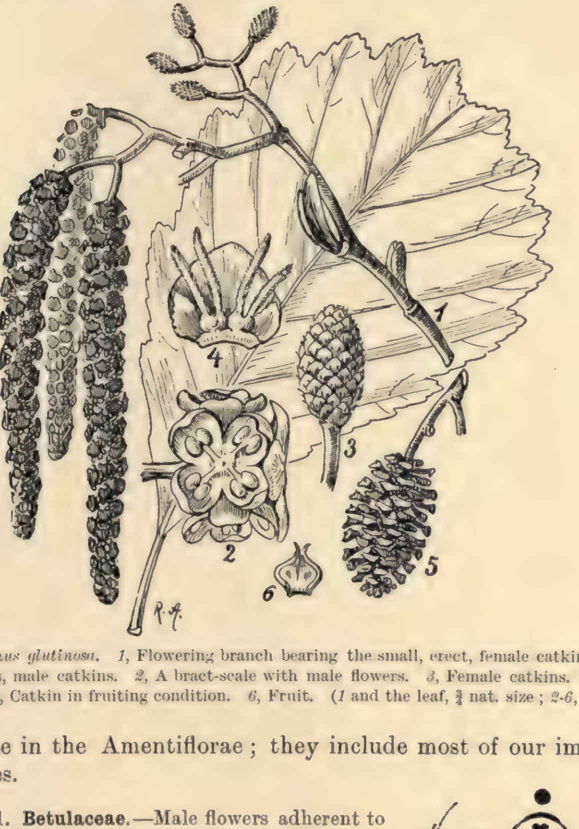


Fig. 562.—*Alnus glutinosa.* *1*, Flowering branch bearing the small, erect, female catkins and the pendulous, male catkins. *2*, A bract-scale with male flowers. *3*, Female catkins. *4* Female flower. *5*, Catkin in fruiting condition. *6*, Fruit. (*1* and the leaf, ¾ nat. size; *2-6*, enlarged.)

Family 1. **Betulaceae.**—Male flowers adherent to the bracts; in catkins. Female flowers in catkins. Ovary bilocular, with two long stigmas; a single, pendulous ovule in each loculus.

Most important Genera.—*Alnus glutinosa*, the Alder, is a prominent tree of damp woods, and is also distributed in swamps and by the banks of streams (Fig. 562). The leaves are bluntly obovate. The inflorescences are already evident in the autumn as stalked catkins, the male long and pendulous, the female erect and short. Male flowers P4, A4; a dichasium of three flowers adherent to each bract (Fig. 563). The female flowers are in pairs, their bracteoles adhering to the bract to form the five-lobed, persistent, woody scale of the cone. *Alnus incana* is distinguished by its leaves being grey and hairy below. *Betula verrucosa* (Fig. 564), the Birch, has a white bark and long-stalked,

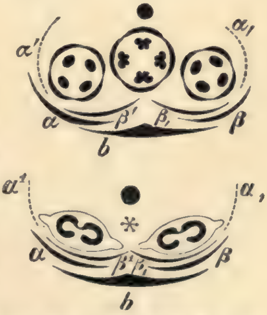


Fig. 563.—*Alnus glutinosa.* Diagrams of Fig. 562, *2* and *4*. Bract *b*; bracteoles $\alpha\,\beta$, $\alpha'\,\beta'$, $\alpha_{,}\,\beta_{,}$. (After Eichler.)

triangular leaves. When young, all the parts are covered with numerous glandular hairs which give the plant an aromatic, resinous odour. The male inflorescences are formed in the autumn of the previous year, singly or a few together, at the tip of shoots of unlimited growth. Flowers P 2, A 2; in dichasia of three, adherent to the bract. Anthers deeply bifid (Fig. 564, 3, 4; Fig. 565). Female inflorescences solitary, at the apex of small, short shoots of the current year. Flowers in dichasia of three in relation to each three-lobed scale; the latter is composed of the bract and the two adherent bracteoles. Fruits borne on pendulous catkins; winged. After the fruits are shed the scales of the catkin separate. *Carpinus Betulus*, the Hornbeam (Fig. 566), is an important forest-tree. The inflorescences appear in spring, the male, from axillary buds of the previous year, either want leaves or are accompanied by one or two, the female are usually terminal. The bract of the male catkin bears 4-10 stamens, bifid to the base, but without bracteoles or perigone. Two female flowers in relation to each bract; each flower with its special bract and pair of bracteoles. The three latter unite to form a three-lobed involucre which serves as an aid to distribution by the wind. *Corylus avellana*, the Hazel (Fig. 567), develops its inflorescences in the preceding year. The male catkins are freely exposed during the winter, while the female remain enclosed by the bud-scales, and only protrude their long red stigmas between the scales at the actual time of flowering. The male flower has no perianth but has a pair of bracteoles which are adherent to the bract, as are the four, deeply bifid stamens (Fig. 568). In the short, female catkins a two-flowered dichasium is present in the axil of each bract as in *Carpinus*; the fringed involucre also is derived from the coherent bracteoles and special bract of each flower (Fig. 568). *Corylus tubulosa* from southern Europe.

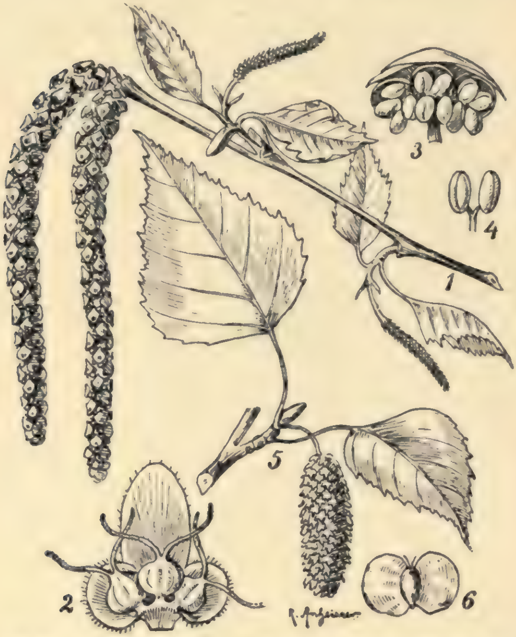


FIG. 564.—*Betula verrucosa.* *1*, Branch with terminal male catkins and female catkins on small lateral branches. *2*, Female flower. *3*, Male flower. *4*, Stamen. *5*, A catkin in fruit. *6*, Fruit. (*1* and *5*, ⅔ nat. size; *2-4* and *6*, enlarged.)

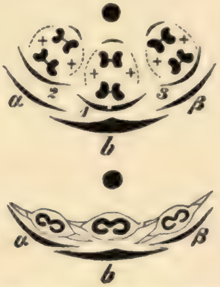


FIG. 565.—*Betula verrucosa.* Diagrams from Fig. 564 3 and 2. *b*, bract; *α β*, bracteoles. (After EICHLER.)

Family 2. **Cupuliferae.**—Inflorescences in the leaf axils, as a rule of shoots of the current year. Flowers with perianth. Ovary trilocular, with three stigmas; two, pendulous, anatropous ovules in each loculus. One or more female flowers are enclosed in a CUPULE formed of coherent bracteoles, which only reaches full development around the fruit. Another interpretation of the cupule is that it corresponds to an outgrowth of the axis bearing numerous reduced leaves (Fig. 569).

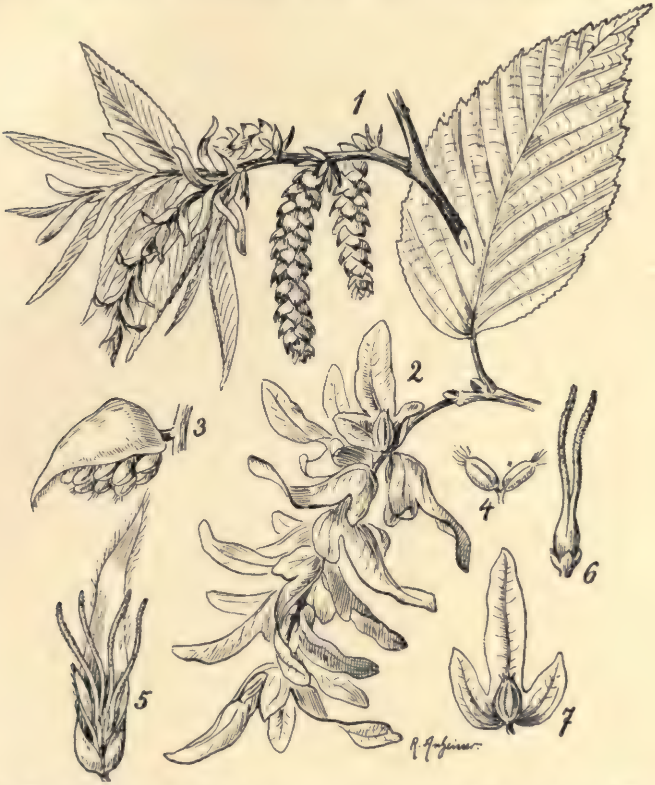


FIG. 566.—*Carpinus betulus.* *1*, Branch with male catkins projecting from the buds of the preceding year and female catkins on the growth of the current year. *2*, Female catkin in fruit. *3*, Male flower. *4*, Stamen. *5*, Bract with two female flowers. *6*, Female flower. *7*, Fruit. (*1*, *2*, *7*, ⅔ nat. size; *3-6* enlarged.)

MORE IMPORTANT SPECIES.—*Fagus sylvatica*, the Beech (Fig. 571), is one of our most important deciduous trees. The leaf is entire, elliptical, shortly stalked, and, especially when young, covered with fine hairs. Leaves two-ranked. Inflorescences on shoots of the current season. Male inflorescences lateral, capitate and pendulous; flower with an oblique, bell-shaped perianth and usually 8-12 stamens. Female inflorescences terminal, capitate and erect; flowers in two-flowered dichasia. The cupule surrounds both flowers (Fig. 570 *B*), and completely

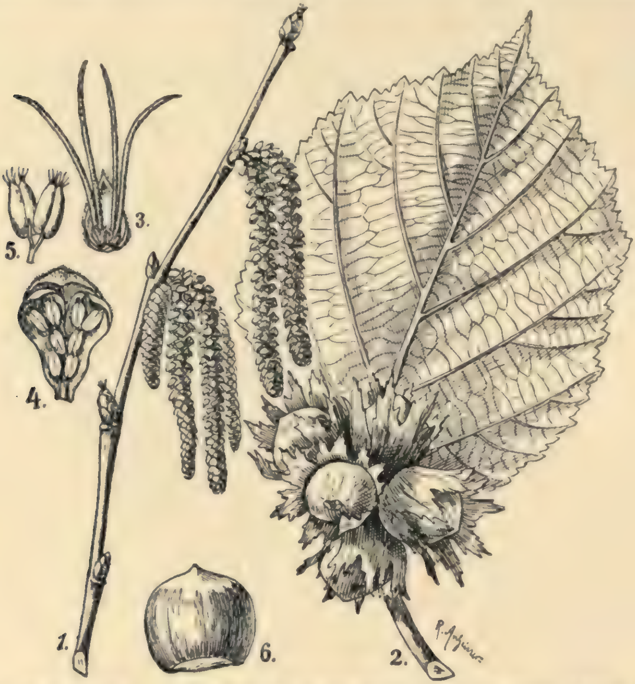


FIG. 567.—*Corylus avellana.* *1*, Branch with male and female catkins. *2*, Group of fruits. *3*, Bract with two female flowers. *4*, Male flower. *5*, Stamen. *6*, Fruit removed from the cupule. (*1*, *2*, *6*, ½ nat. size; *3*-*5* enlarged.)

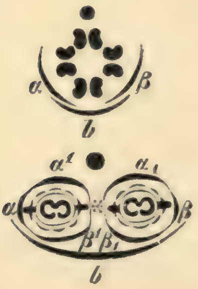


FIG. 568.—*Corylus avellana.* Diagram of Fig. 567, *3* and *4*. *b*, bract. $\alpha\beta$, $\alpha'\beta'$. $\alpha_{,}$ $\beta_{,}$, bracteoles. (After EICHLER.)

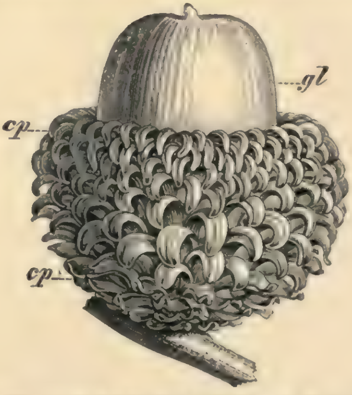


FIG. 569.—Cupule of *Quercus Aegilops.* *cp*, cupula; *gl*, fruit. (After DUCHARTRE.)

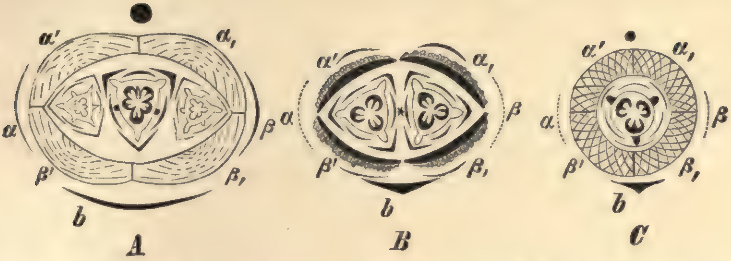

α'
$\alpha_{,}$
α
β
β'
$\beta_{,}$
b
A
α'
$\alpha_{,}$
α
β
β'
$\beta_{,}$
b
B
α'
$\alpha_{,}$
α
β
β'
$\beta_{,}$
b
C

FIG. 570.—Diagrams of the female dichasia of: *A*, *Castanea vulgaris*; *B*, *Fagus sylvatica*; *C*, diagram of the single flower of *Quercus pedunculata*. *b*, Bract; α β, bracteoles; $\alpha_{,}$ $\beta_{,}$, α′ β′, bracteoles of the secondary flowers adherent to the cupule. (After EICHLER.)

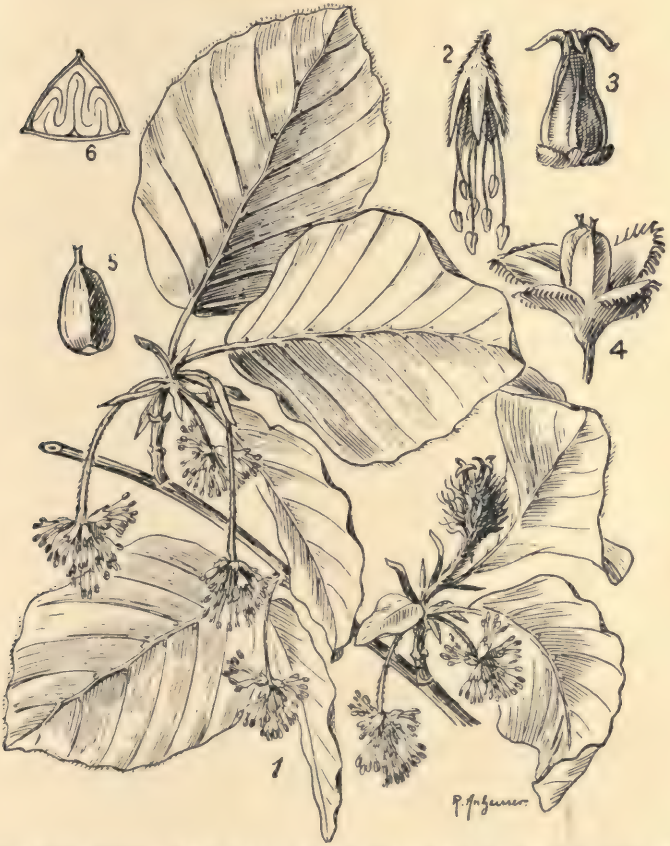


FIG. 571.—*Fagus sylvatica*. (⅔ nat. size.) *1*, Branch with male and female inflorescences. *2*, Male flower. *3*, Female flower. *4*, Open cupule with two fruits. *5*, Fruit. *6*, Transverse section of a fruit showing the folded cotyledons of the embryo. (*2*, *3*, *6*, enlarged.)

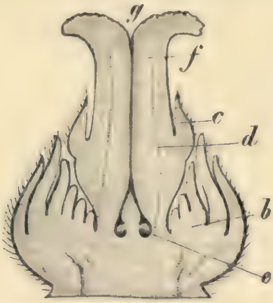


FIG. 572.—*Quercus pedunculata*, longitudinal section of the female flower. *b*, The young cupule; *e*, ovule; *d*, ovary; *c*, perigone; *f*, style; *g*, stigma. (After BERG and SCHMIDT, magnified.)

envelops the triangular, nut-like fruits; at maturity it opens by splitting into four valves. The surface is covered with numerous, blunt prickles.

Castanea vulgaris, the edible Chestnut, is a native of the Mediterranean region. The inflorescences on shoots of the current year bear in some cases only male flowers, in others female flowers at the base and male flowers above. Flowers grouped in dichasia. Female dichasia three-flowered (Fig. 570 *A*), so that three nuts come to be enclosed within the spiny cupule, which splits into four valves. The Oaks, *Quercus pedunculata* (Figs. 572, 573) and *Quercus sessiliflora*, are the largest deciduous trees of European woods. Leaves

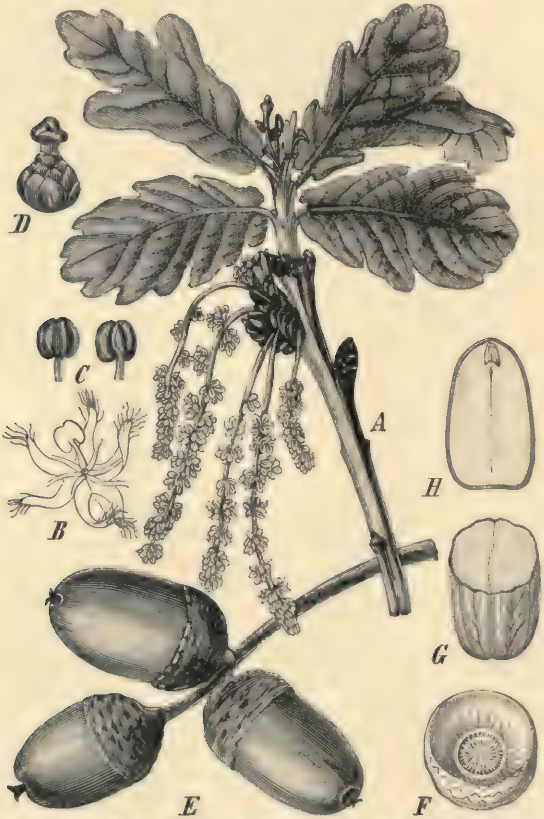


FIG. 573.—*Quercus pedunculata*. *A*, Flowering branch; *B*, a male flower (magnified); *C*, stamens (magnified); *D*, a female flower (magnified); *E*, infructescence; *F*, cupule; *G*-*H*, seed.

oval, margins sinuately lobed; those of *Q. sessiliflora* with longer stalks. The pendulous, male inflorescences spring at the time that the new foliage is expanding from axillary buds of the shoot of the preceding year or from the lowest buds of the shoot of the current year; flowers solitary, consisting of a perianth of 5-7 segments and 6-12 short stamens. Female inflorescences erect, few-flowered, in the axils of the upper leaves of the shoot of the current year. Flowers solitary; in *Q. pedunculata* with long stalks, in *Q. sessiliflora* sessile. Each flower is invested by a cupule (Fig. 570 *C*), which is at first inconspicuous, but is fully developed on the ripe fruit.

The Beech yields firewood, tar, and pyroligneous acid; the Oak provides a valuable timber, a bark containing tannin used in tanning, and cork from the Cork-oak.

OFFICIAL.—The GALLS produced on the young twigs of *Quercus infectoria* as a result of puncture by the Gall-wasp *Cynips tinctoria*; Tannic Acid is obtained from these.

Order 5. Urticinae

Herbaceous or woody plants with small, inconspicuous flowers closely aggregated in the inflorescence. Mainly anemophilous. Perianth simple, sepaloid. Stamens equal in number to the leaves of the perigone and superposed on the latter. Ovary superior, composed of one or two carpels, usually unilocular, and containing a single ovule. Fruit, a nut or drupe. Seeds usually containing endosperm.

Family 1. **Ulmaceae.**—Trees or shrubs with simple, asymmetrical leaves borne in two rows. The pinnate venation, the hairy surface, the serrate margin of the leaf and the caducous stipules are characteristic. Flowers in clusters in the axils of leaves of the previous year, hermaphrodite, or unisexual by suppression of the male or female organs. Perigone of 4-6 leaves, with a corresponding number of stamens situated opposite to them. Stamens straight in the bud. Unilocular ovary composed of two carpels with one pendulous ovule.

Ulmus campestris (Fig. 574), the Elm, is a common European tree. The arrangement of the leaves on the sides of the twigs in two rows and the corresponding branching leads to the leaf-surface exposed by each lateral branch making a definite angle with the main branch and composing the regular convex crown of foliage exhibited by older examples. The tree flowers in February and the fruits ripen before the leaves expand. The fruits are broadly winged and adapted to be carried by the wind. *U. montana*, *U. effusa* are closely related forms. Several species of *Celtis*, in which the fruit is a drupe, are in cultivation.

Family 2. **Moraceae** (16).—The majority are trees or shrubs with abundant latex. Leaves alternate, stipules caducous. Flowers unisexual in globular or disc-shaped inflorescences; usually P4, A4, and P4, $G(\underline{2})$. Stamens opposite the leaves of the perigone. Ovary bicarpellary, unilocular, with one, pendulous, anatropous ovule.

IMPORTANT REPRESENTATIVES.—In addition to the Mulberry trees, of which *Morus alba* is cultivated for the rearing of Silk-worms and *M. nigra* as a fruit-tree, the genus *Ficus* deserves special mention. The species occurring farthest north is the Common Fig (*Ficus carica*, Fig. 575), which is endemic to the Mediterranean region, and has been long cultivated. It is a low tree with palmately incised leaves and stipules, which form a cap-like protection to the bud. The inflorescences are hollow, pitcher-shaped structures with a narrow opening. The flowers are borne closely crowded together on the inner surface. The flat, disc-shaped inflorescences of *Dorstenia* which bear the flowers on the upper surface, are in many respects corresponding structures (17). The pollination of the Fig is effected by a species of wasp, which lays its eggs in the short-styled female flowers or gall-flowers. The sweet, fleshy portion of the edible Fig is developed from the hollowed axis of the inflorescence together with the perigones of the individual flowers. The small, hard, seed-like bodies are the fruits developed from the ovaries of the small flowers. Some species of *Ficus* are among the largest trees of tropical forests.

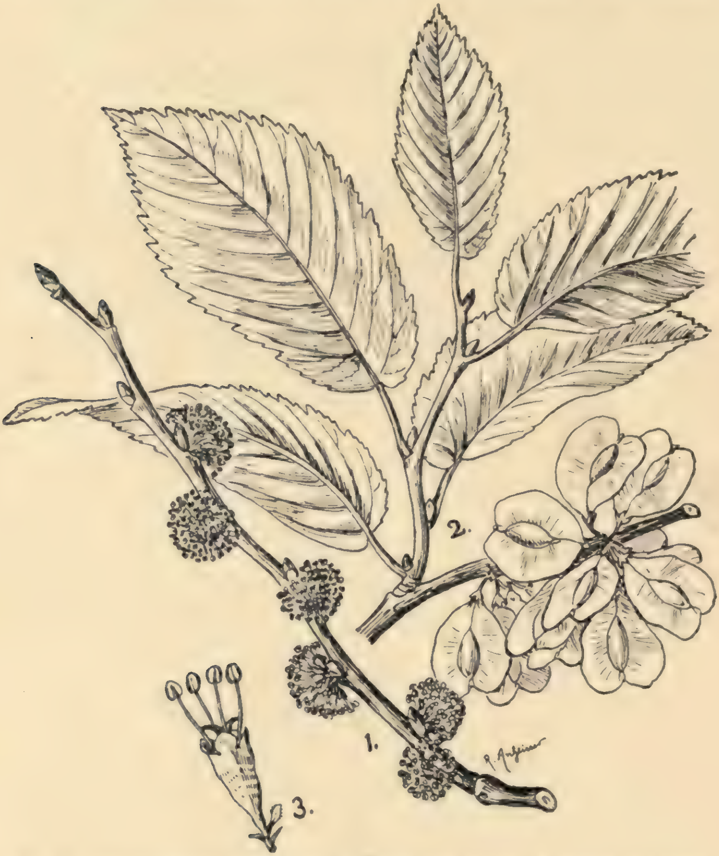


FIG. 574.—*Ulmus campestris* ($\frac{2}{3}$ nat. size). *1*, Branch with flowers. *2*, Branch with fruits. [*3*, Single flower, enlarged.]

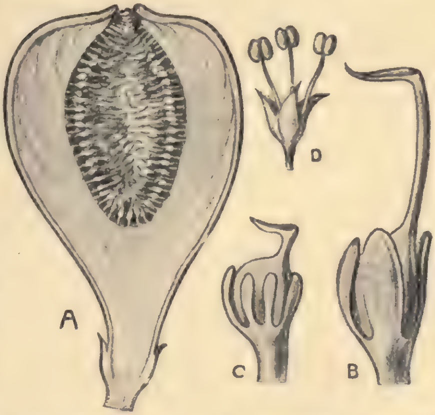


Fig. 575.—*Ficus carica.* *A*, Longitudinal section of an inflorescence. *B*, Fertile flower. *C*, Gall-flower. *D*, Male flower. (*B-D*, enlarged; *D*, after Kerner; *B*, *C*, after Solms-Laubach.)

The most remarkable is the Banyan (*Ficus bengalensis*), which occurs in the East Indies. The seeds, carried by fruit-eating birds, germinate on the branches of trees, where the plant develops as an epiphyte. The proper form of the tree is only seen, however, after the roots have reached the soil, and it is no longer dependent on the scanty food supply obtainable in the epiphytic position. The host-plant is gradually strangled, additional roots are sent down to the soil and thicken into pillar-like supports, and ultimately a small wood capable of sheltering an entire village is developed from the single small seedling. The latex of *Ficus elastica* is obtained from the tree by making incisions in the bark, and serves as one source of india-rubber. *Castilloa elastica* is another important rubber-tree of Central America. The gigantic inflorescences when in

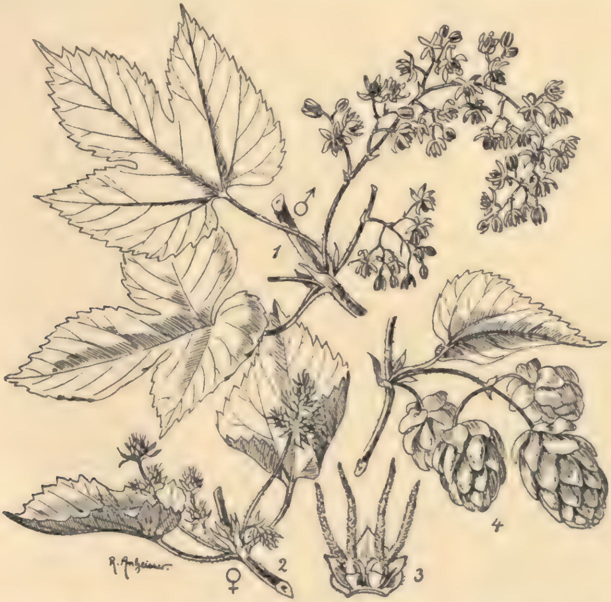


Fig. 576.—*Humulus lupulus.* *1*, Male inflorescence. *2*, Female inflorescence. *3*, Two female flowers in the axil of a bract. *4*, Cone-like inflorescences in fruit. (½ nat. size.)

fruit of species of *Artocarpus* are eaten raw or cooked and form the Bread-fruit of the Tropics. The species of *Cecropia* are American, myrmecophilous trees (cf. p. 235).

OFFICIAL.—The fruits of *Ficus carica*.

Family 3. **Cannabinaceae.**—Annual or perennial herbs without latex, with palmately veined leaves and free, persistent stipules. Diœcious. Male flowers P 5, A 5; stamens straight in the bud. The male inflorescences are dichasia, the central branch capable of further growth. The female flowers have a slightly developed, entire perianth. Ovary bicarpellary, with two large feathery stigmas; unilocular, with a pendulous, anatropous ovule. Anemophilous. Fruit, nut-like. Embryo curved.

GENERA.—*Humulus lupulus*, the Hop, is a native of central Europe; it has a perennial rhizome, which annually produces a crop of twining shoots (Fig. 576). The stem and opposite leaves bear coarse hairs, and the former bears hooked prickles which prevent it slipping down the support. The branches of the female inflorescence are catkin-like, the scales being formed of the pairs of stipules belonging to bracts of which the laminae are suppressed. The axillary shoot of the bract is also suppressed, but each stipule has two flowers in its axil; each flower is enclosed by its own bract. These bracts project beyond the stipules when the inflorescence is mature, and give the latter its cone-like appearance. Upon them are developed the glandular hairs on account of which the Hop is cultivated.

Cannabis sativa, Indian Hemp, is an annual herb with palmately divided, hairy leaves, which are opposite below and alternate in the upper portion of the shoot. The female inflorescence resembles that of the Hop, but the central shoot, which in that plant is suppressed, grows out in the Hemp to a leafy shoot. Only a single flower is present in the axil of each bract. The same process is repeated in the axil of each leaf of the leafy, middle shoot, so that the whole female inflorescence is a repeatedly branched structure. The plant is utilised in Europe for its bast fibres, which are from one to several centimetres long [17a]. The glandular hairs which cover all parts of the female inflorescence secrete a sticky resinous substance which is used medicinally. In the East it is used in the preparation of a narcotic called Haschisch.

OFFICIAL.—*Cannabis sativa* provides CANNABIS INDICA. *Humulus lupulus* provides LUPULUS and LUPULINUM.

Family 4. **Urticaceae.**—Perennial herbs or less commonly shrubs. Leaves simple, stipulate. Flowers unisexual by suppression of parts, as a rule bimerous. P 2+2, A 2+2. Stamens inflexed in the bud, and scattering the pollen when they suddenly straighten. Ovary consisting of a single carpel, unilocular, with a basal, atropous ovule. Perianth of the female flower adherent. Flowers in dichasia, or crowded in dorsiventral inflorescences. Anemophilous.

A number of the Urticaceae are characterised by the possession of stinging hairs (cf. Fig. 116), *e.g.* the common Stinging Nettles, *Urtica dioica* and *U. urens*, and the dangerous tropical species of *Laportea*. Some provide important fibres, especially *Boehmeria nivea* from which Ramie fibre is obtained, and, of less value, *Urtica cannabina*, and our native species of *Urtica*.

Order 6. Centrospermae

Herbs, less commonly small woody plants. Flowers with few exceptions hermaphrodite and tri- or penta-merous. Perianth and androecium consisting of one or two whorls. Ovary superior, unilocular, with a single basal ovule or with a free central placenta bearing a number of ovules.

Family 1. **Polygonaceae.**—For the most part perennial herbs, with hollow stems swollen at the nodes, and alternate, simple leaves. The membranous stipules of the latter are coherent to form a sheath or OCHREA protecting the terminal bud; when broken through by the growth of the stem this remains as a tubular sheath around the lower part of the internode (Fig. 577). The hermaphrodite flower is typically trimerous, but a larger number of members sometimes occurs in the perigone or the androecium. Ovary superior, formed of three carpels, unilocular, with a single, basal, atropous ovule. Fruit in nearly all cases a triangular nutlet.

GENERA.—*Rheum*, Rhubarb. This is an East Asiatic genus, with large, radical leaves and a large, spreading, paniculate inflorescence (Fig. 578). Leaves simple, cordate-reniform, with palmate venation, sometimes more or less lobed. The flower has a perigone of two similar whorls, and two whorls of stamens, the outer whorl being double by chorisis; P 3 + 3, A 6 + 3, G $\underline{(3)}$. Nectar for visiting insects is secreted by the large scales of the disc. The triangular ovary becomes winged as it develops into the fruit (Fig. 579). Species of *Rheum* are cultivated as ornamental plants and as vegetables. *Rumex acetosa*, Sorrel, with sagittate leaves. The structure of the flowers of the hermaphrodite species of *Rumex* is similar to that of *Rheum*, but the inner whorl of stamens is wanting. The species of *Polygonum* have a perigone consisting of five, coloured leaves and a varying number of stamens. The triangular fruits of *Fagopyrum esculentum* form Buckwheat (Fig. 508).

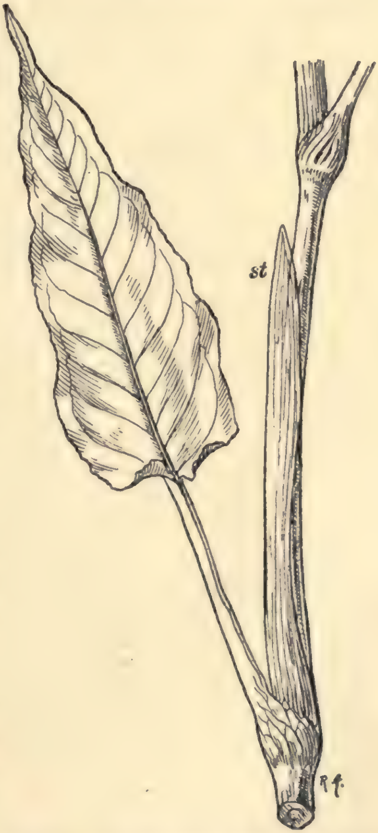


FIG. 577.—Leaf of *Polygonum amplexicaule* showing the ochrea (*st*). (½ nat. size.)

OFFICIAL.—The rhizome of *Rheum officinale*, *Rh. palmatum*, and probably other species yields RADIX RHEI.

Family 2. **Chenopodiaceae.**—Perennial or annual herbs, rarely small woody plants, with alternate leaves. Flowers typically pentamerous, with a single whorl in both perigone and androecium; P5, A5, G (2-5). Reduced, unisexual flowers are not infrequent.

The unilocular ovary contains a basal, campylotropous ovule. Fruit, a nut. Seed with a curved embryo bent around the perisperm.

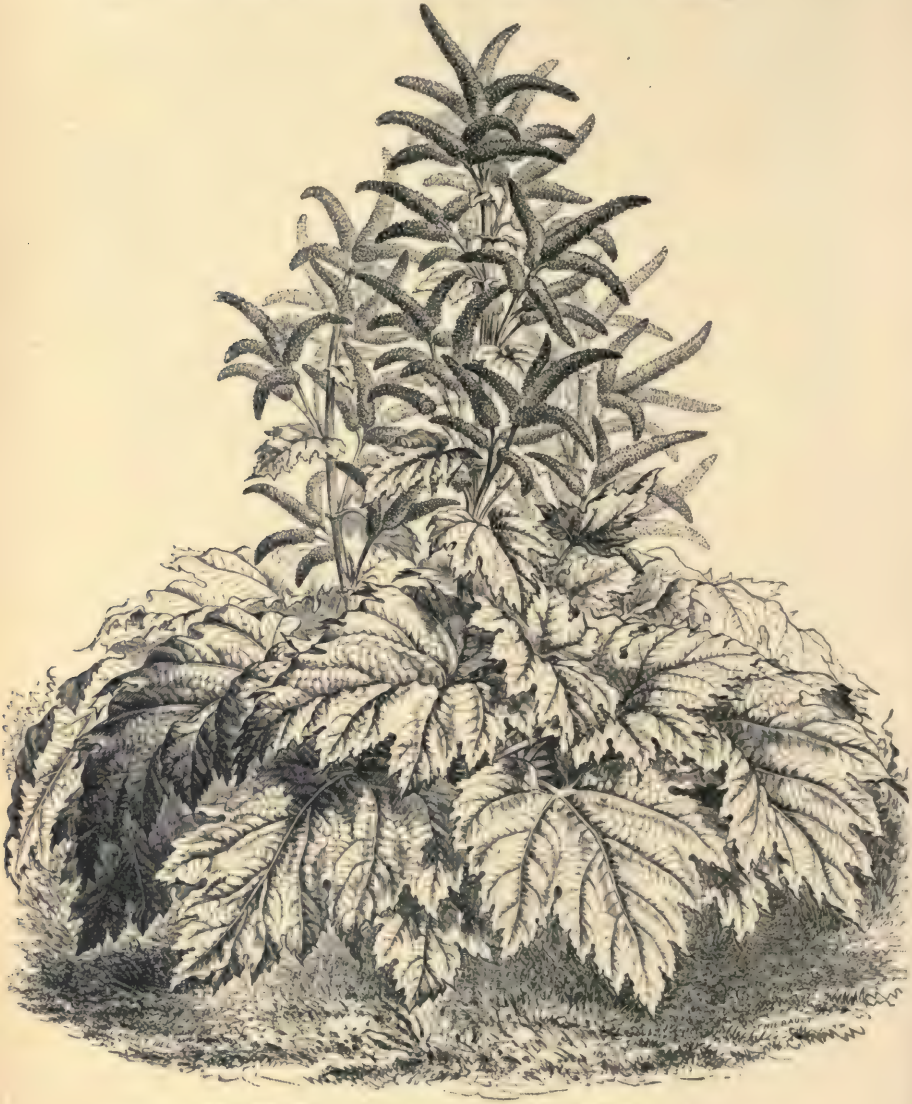


FIG. 578.—*Rheum officinale*, greatly reduced. (After BAILLON.)

Many of the Chenopodiaceae are strand plants or occur on soils containing a large amount of salt, such as the great Asiatic salt steppes and deserts (18). The Spinach (*Spinacia oleracea*) is used as a vegetable. The Sugar Beet (*Beta vulgaris*, var.

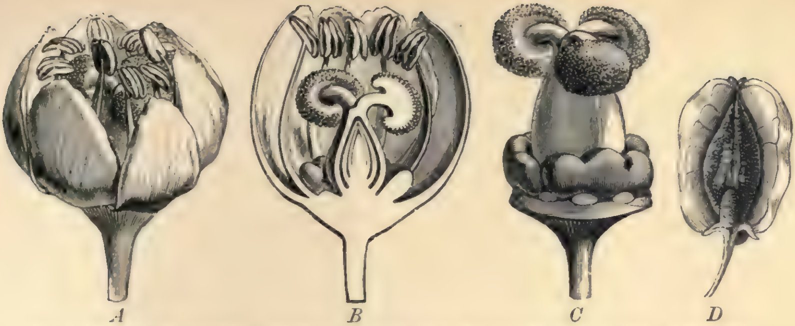


FIG. 579.—*Rheum officinale.* *A*, Flower; *B*, the same cut through longitudinally; *C*, gynaeceum with disc. *Rheum compactum*: *D*, fruit. (After LÜRSSEN, magnified.)

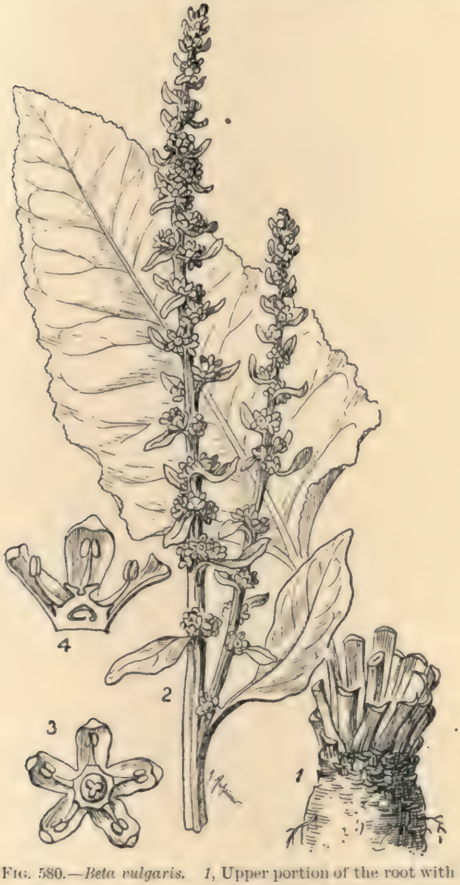


FIG. 580.—*Beta vulgaris.* *1*, Upper portion of the root with the rosette of leaves, the blades of which are cut off. (Greatly reduced.) *2*, Branch of the inflorescence (½ nat. size). *3*, Flower cut through longitudinally (*3* and *4* enlarged.)

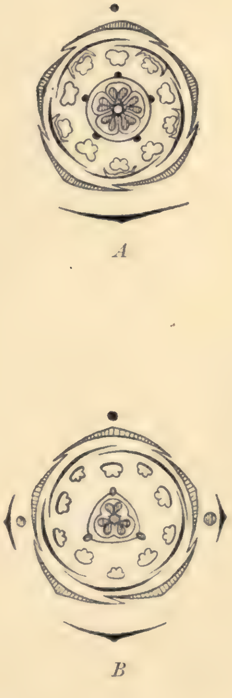


FIG. 581.—Diagrams of the Caryophyllaceae. *A*, *Viscaria*, septa present in the lower part of the ovary; *B*, *Silene*, septa absent. (After EICHLER.)

rapa) (Fig. 580) is a plant of great economic importance. It is a biennial plant, and in the first season forms a thick, swollen root bearing a bud consisting of a number of thick-stalked, entire, succulent, and often crisped leaves. From this rosette of leaves there springs in the second season a highly branched panicle, bearing the inconspicuous greenish flowers. Ovary formed of three carpels. At the end of the first season the root contains cane-sugar as a reserve material, which at this stage is extracted from the plant. By constant selection the percentage of sugar is raised from 7-8% to an average of 14%; it may, however, reach 21-26%. The original form of the Sugar Beet is *Beta patula*. *Chenopodium* and *Atriplex* are common weeds near human dwellings.

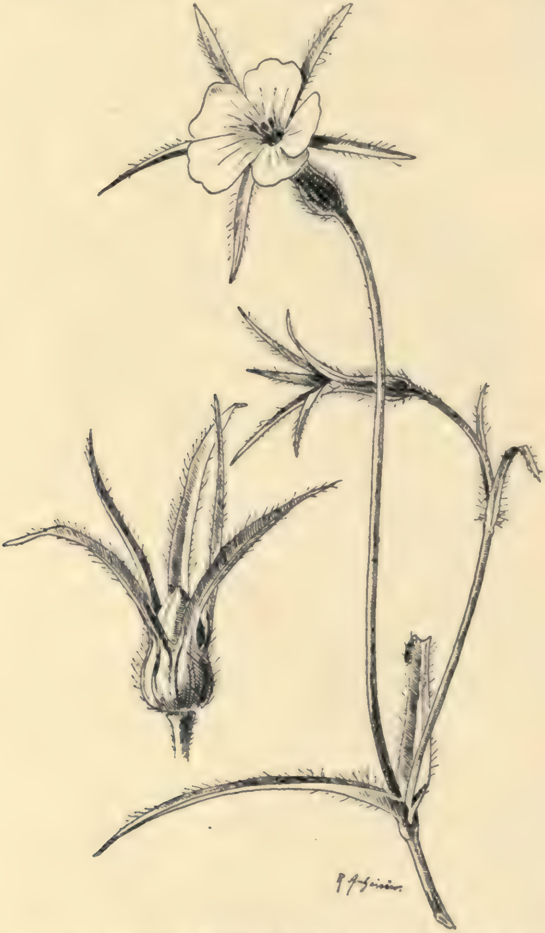


FIG. 582.—*Agrostemma Githago*. Flowering shoot and fruit ($\frac{1}{2}$ nat. size). *POISONOUS.*

Family 3. **Caryophyllaceae.**—Annual or perennial herbs, very rarely shrubs, with simple, linear, usually opposite leaves; flowers typically pentamerous, with calyx and corolla. Two whorls of stamens, obdiplostemonous. Unilocular or incompletely septate ovary. K 5, C 5, A 5 + 5, G (5). Fruit, a capsule. Seeds numerous, embryo curved around the floury perisperm. In reduced forms the fruit is nut-like (Figs. 581-583).

SUB-FAMILIES AND GENERA.—1. *Alsineae* — Calyx polysepalous; petals with short claws; fruit, a capsule. *Cerastium*, *Spergula*, with pentamerous flowers; *Stellaria* and *Arenaria* with tri-carpellary ovary. 2. *Paronychieae.* Calyx polysepalous; corolla wanting or inconspicuous; fruit nut-like. *Scleranthus*, *Herniaria.* 3. *Sileneae.* Calyx gamosepalous; petals with long claws, fruit a capsule. *Lychnis* and *Agrostemma* with five carpels, *Silene* with three, *Dianthus* and *Saponaria* with two. *Cerastium* and *Stellaria* have white flowers with bifid petals and are conspicuous, early-flowering forms. Species of *Dianthus*, Pinks, have frequently attractive colours and scent, and occur in dry sunny situations. *Agrostemma Githago* (Fig. 582), Corn-cockle, is a hairy plant with pink flowers; it is a common weed in corn-fields. Since its seeds are poisonous, their mixture with the grain may have serious results. *Saponaria officinalis* occurs especially by the banks of streams; it is a herb attaining the height of a metre, with opposite, broad leaves and rose-coloured flowers. The saponin contained in all parts of the plant renders it poisonous (Fig. 583).

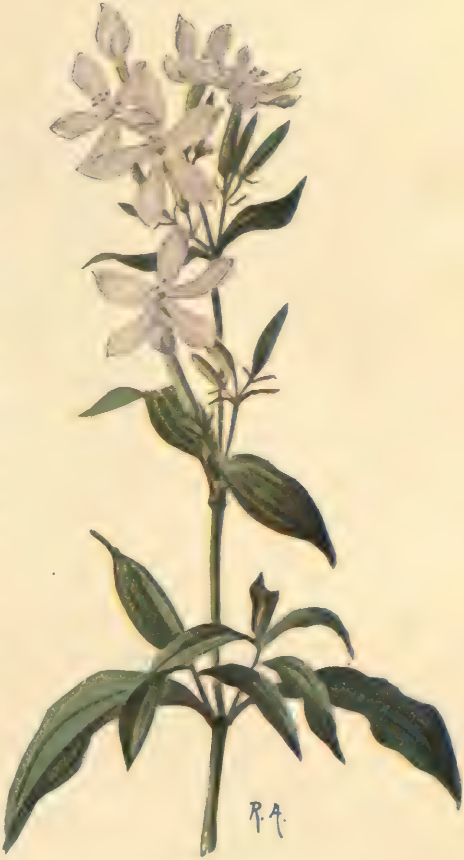


FIG. 583.—*Saponaria officinalis* (½ nat. size). *POISONOUS.*

Order 7. Polycarpicae

This large order includes a number of families of very different general appearance but exhibiting as common characters a superior gynaeceum with the carpels free from one another, and a spiral arrangement of the members of the flower. The tendency to considerable increase in the number of stamens stands in relation to this.

It is, however, to be noted that by no means all the plants of the families united in this order exhibit the above characters in the same degree. The characteristic features may indeed be completely wanting, though the existence of intermediate forms leaves no doubt that the genera in question must be classed here.

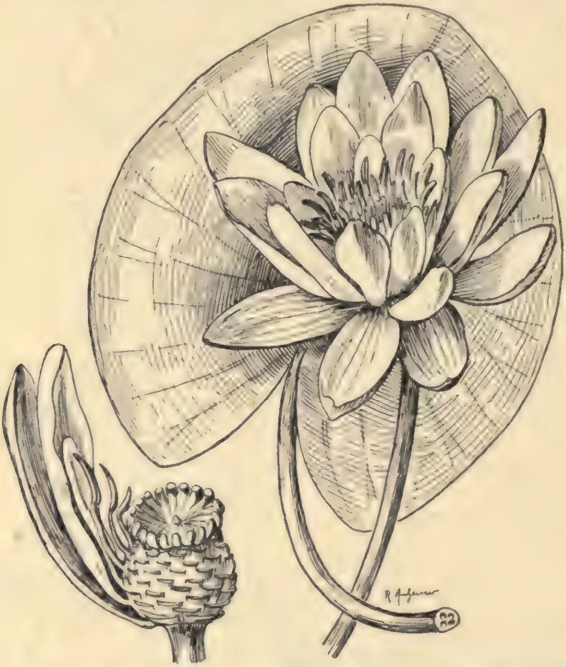


FIG. 584.—*Nymphaea alba* (½ nat. size). The spiral arrangement of the stamens and petals is shown by their insertions on the ovary to the left.

Family 1. **Nymphaeaceae** (19).—Aquatic plants with submerged or floating leaves, the latter often of very large size ; when both types of leaf are present there is more or less marked heterophylly. Flowers hermaphrodite, with calyx and corolla. The whorls consist of three (rarely), four, or more numerous members. Carpels sometimes free. Parts of the flower often spirally arranged (Figs. 584-586). Latex.

Nymphaea alba, the White Water Lily (Fig. 584), has large floating leaves and white flowers, protected by firm green sepals. Within the corolla comes the zone of numerous stamens and the inferior ovary composed of numerous, coherent carpels. The spiral arrangement of the members of the perianth and androecium is seen by the scars of their insertion when they are removed from the inferior ovary (Fig. 584), and in the floral diagram (Fig. 585). In *Nuphar* the ovary is superior and the small petals bear nectaries; the conspicuous calyx renders the flower attractive. In the American genus *Cabomba* the flowers are trimerous and the pistil is apocarpous. The finely divided, submerged leaves differ in appearance from the entire, floating leaves. The carpels are also free in *Nelumbium*, both the leaves and flowers of which are raised above the surface of the water. *Victoria regia* from the Amazon, and *Euryale ferox* from tropical Asia, have gigantic floating leaves; they are often cultivated in Botanic Gardens.

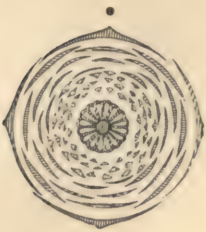


FIG. 585.—*Nymphaea*. Floral diagram.

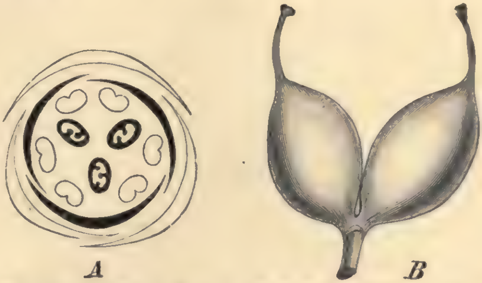


FIG. 586.—*A*, Floral diagram. *B*, Fruit of *Cabomba aquatica* showing two carpels developed as partial fruits. (After BAILLON. × 4.)

The family of the **Ceratophyllaceae** with the single genus *Ceratophyllum* may be placed here. The plants which often occur in masses are submerged aquatics.

Family 2. **Ranunculaceae** (20).—Herbs or rarely woody plants with alternate, exstipulate leaves. Flowers hermaphrodite, the members in many cases arranged spirally. Perianth either forming a simple perigone or differentiated into calyx and corolla. Stamens indefinite. Pollen-grains with at least three places of exit for the pollen-tubes. Carpels three to indefinite, borne on the convex receptacle, and forming an apocarpous, superior ovary. Ovules, borne on the ventral suture, singly or in numbers. The partial fruits are follicles, achenes, or berries. Seed with a small embryo enclosed within the large, oily endosperm (Figs. 587-597).

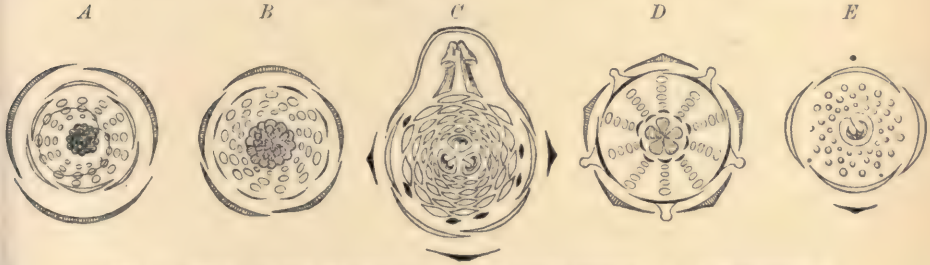


FIG. 587.—Floral diagrams of Ranunculaceae. *A*, *Anemone nemorosa*. *B*, *Adonis autumnalis*. *C*, *Aconitum napellus*. *D* *Aquilegia vulgaris*. *E*, *Cimicifuga racemosa*. (After EICHLER.)

Important Genera.—Many of our commonest meadow and woodland plants belong to this order. They are all in greater or less degree poisonous. Numerous species of *Ranunculus,* characterised by the usually yellow flowers, convex receptacle, and fruit composed of numerous free achenes, occur in Britain. The petals have a nectary at the base. Leaves palmately divided more or less deeply. *R. sceleratus* is very poisonous (Fig. 590). *R. arvensis* with large, spiny achenes or nutlets (Fig. 589). The aquatic species of *Ranunculus,* belonging to the section *Batrachium,* are often heterophyllous (Fig. 35, p. 34), the floating leaves serving to support the flowers above the surface of the water.

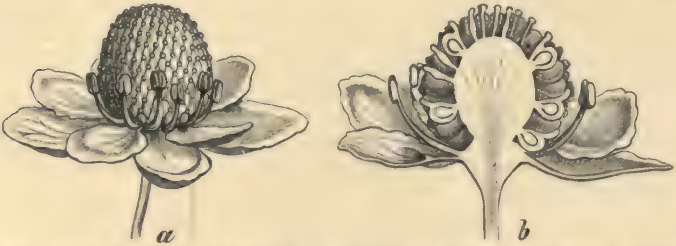


Fig. 588.—Flower of *Ranunculus sceleratus* ; *b,* the same, cut through longitudinally ; magnified. (After Baillon.)

Species of *Anemone* are also widely distributed in Europe. *A. nemorosa* occurs commonly in woods and is one of our early spring flowers. It has a horizontal, subterranean rhizome, which terminates in a flower, the further growth of the plant being carried on by a lateral shoot. Perianth simple, petaloid. All species of *Anemone* have at a greater or less distance from the perianth a whorl of, usually, three leaves forming an involucre (Fig. 591). In *A. hepatica* this stands just below the perianth and thus resembles a calyx. All the species are to some extent poisonous, especially *A. Pulsatilla.* Many are valued and are cultivated in quantity during winter, especially on the Riviera, to supply the market with cut flowers. The plants of the genus *Clematis* are mostly woody and differ from other Ranunculaceae in having opposite leaves. Many species are cultivated. *C. vitalba* is one of our few native lianes. The achenes of the species of *Clematis* and of many kinds of *Anemone* are provided with hairy or feathery appendages, which facilitate their distribution by the wind. The floral axis in the Mouse-tail (*Myosurus*) is greatly elongated and the spiral arrangement of the small achenes upon it is very evident. *Thalictrum* has large, showy stamens, and the perianth is readily shed (on apogamy in this genus, cf. p. 518). *Caltha palustris,* the Marsh Marigold (Fig. 592), is one of the most conspicuous spring flowers in damp meadows. Perianth simple, bright yellow. Leaves cordate or reniform, short-stalked, with erect sheathing base. Fruit composed of follicles. *Helleborus foetidus* (Fig. 593) has firm, palmately divided leaves. The prominent inflorescence bears in January or February greenish flowers which stand in the axils of the broadly sheathing, three-toothed bracts and are spirally constructed throughout. The five large sepals persist until the fruit is ripe. The petals,

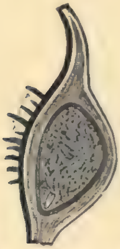


Fig. 589.—*Ranunculus arvensis.* Carpel in longitudinal section. (After Baillon, enlarged.)

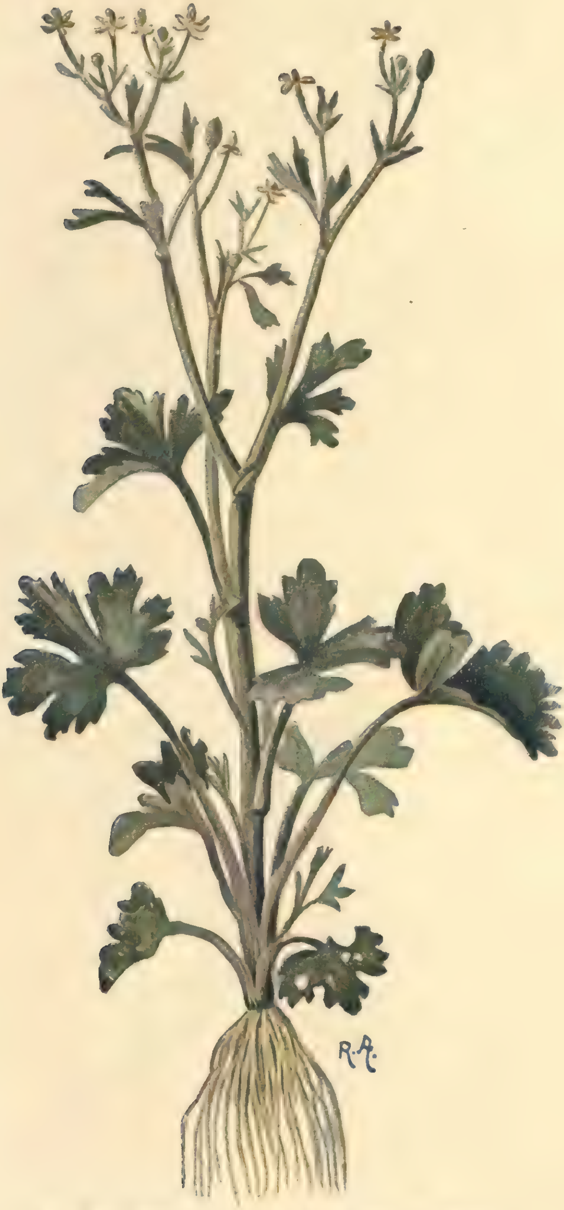


FIG. 590.—*Ranunculus sceleratus* (½ nat. size). *POISONOUS.*

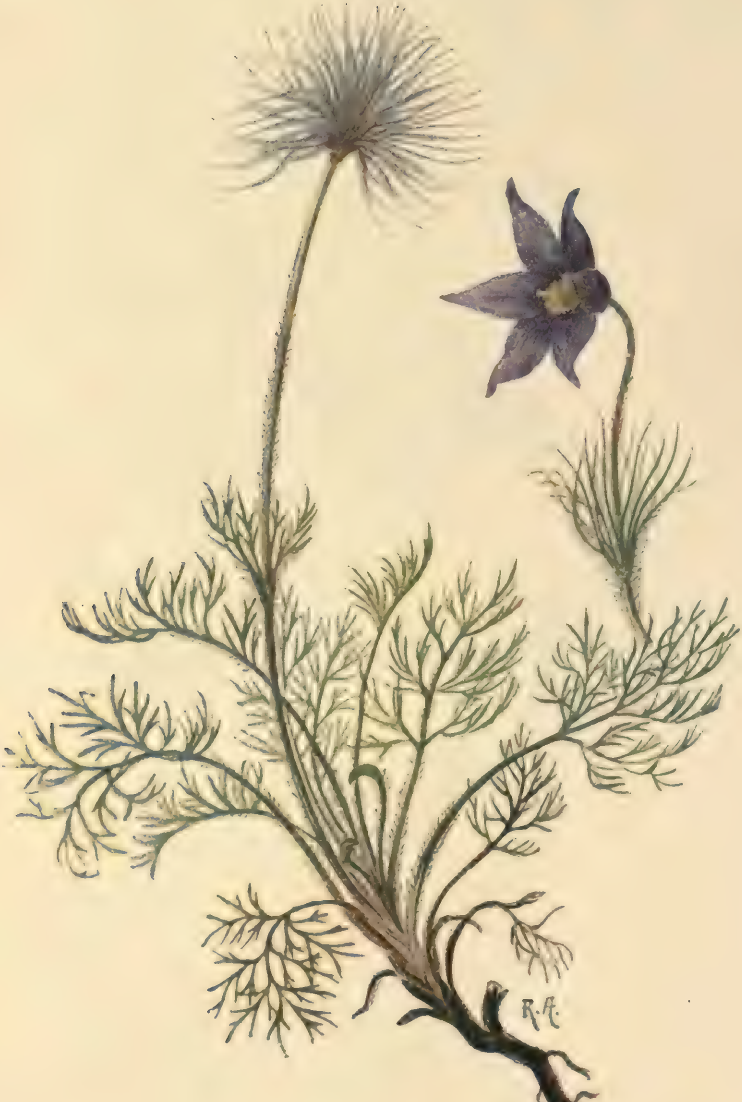


FIG. 591.—*Anemone Pulsatilla* (½ nat. size). *POISONOUS.*

which are usually thirteen in number, have the form of tubular, two-lipped nectaries. Numerous stamens. Carpels 3-5, developing into follicles. *Helleborus niger*, from the south-eastern Alps, flowers in autumn and winter and is commonly cultivated. *Helleborus viridis.* All three species are poisonous. The Monkshood (*Aconitum napellus*) is a stately perennial herb with underground tubers and occurs most commonly in alpine meadows. The leaves are palmately divided, the segments being in turn pinnately lobed (Fig. 595) and widened towards the tip. Inflorescence a dense raceme, reinforced by lateral inflorescences standing in the axils of the upper leaves. Flowers zygomorphic. One of the five, dark blue sepals is helmet-shaped, and protects two long-stalked, tubular, two-lipped nectaries, which correspond to petals. The remaining petals are wanting or are reduced to inconspicuous, narrow structures (Fig. 594). *Aconitum lycoctonum* (Fig. 596) has smaller, yellow flowers of similar construction. *A. Stoerkianum* and *A. variegatum* resemble *A. napellus* but are more brightly coloured. All the species are poisonous. *Aquilegia*, *Delphinium* and *Paeonia* are favourite ornamental plants with showy flowers. In *Actaea* the fruit is a berry.

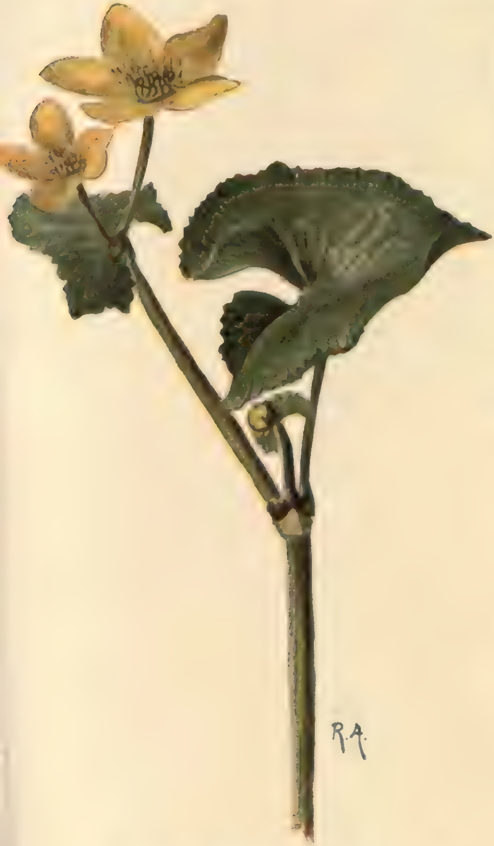


FIG. 592.—*Caltha palustris* (⅔ nat. size). *POISONOUS.*

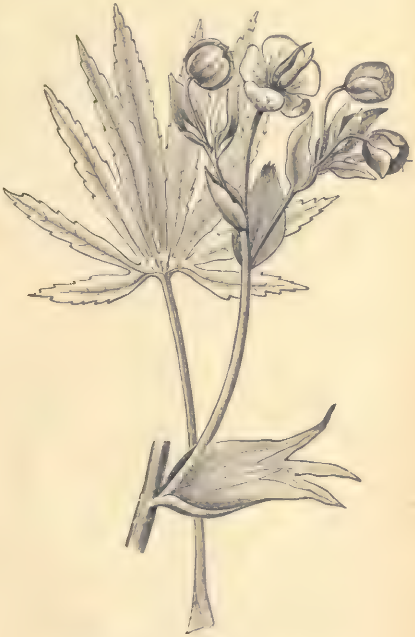


FIG. 593.—*Helleborus foetidus* (⅓ nat. size). *POISONOUS.*

OFFICIAL.—ACONITI RADIX is obtained from *Aconitum napellus*. STAPHISAGRIAE SEMINA from *Delphinium staphisagria*. CIMICIFUGAE RHIZOMA from

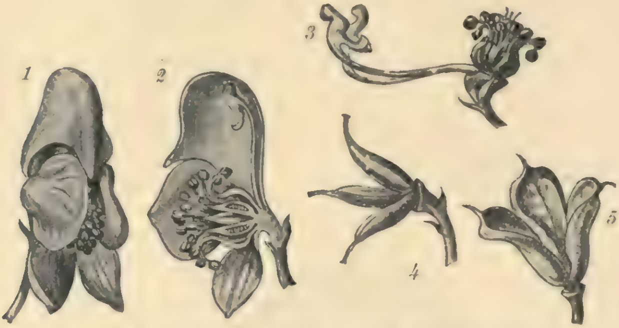


FIG. 594.—*Aconitum napellus* (nat. size). *1*, Flower seen obliquely from in front. *2*, Flower in longitudinal section. *3*, The nectaries, formed from petals, and the androecium after the perigone has been removed. *4*, Fruit composed of three apocarpous carpels. *5*, Follicles opened.

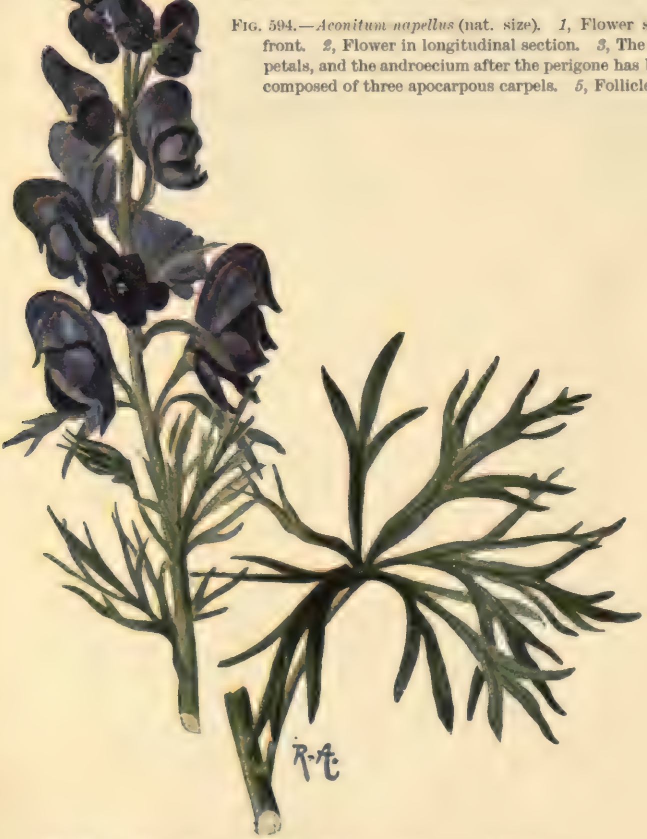


FIG. 595.—*Aconitum napellus* (½ nat. size.) *OFFICIAL* and *POISONOUS*.

Cimicifuga racemosa. HYDRASTIS RHIZOMA from the North American *Hydrasti canadensis* (Fig. 597), a perennial herb which sends its subaerial shoots up from the subterranean rhizome; the base of the shoot has keeled scale leaves in two ranks. The flowers are solitary and terminate the shoots, each of which bears two foliage leaves. The simple, white perianth falls when the flower opens. The androecium and the apocarpous gynaeceum consist of numerous members. The fruit consists of numerous, small berries, each of which includes 1-2 seeds. The alkaloid HYDRASTINE is obtained from the rhizome.

Family 3. **Magnoliaceae.**—Woody plants from tropical and temperate America and Asia. The leaves are alternate and usually provided with stipules, which protect the structures in the bud. Flowers and fruit as in the Ranunculaceae, but the pollen-grains have only one place of exit for the pollen-tube. Oil-cells in stem and leaf. Species of *Magnolia* are largely cultivated on account of their showy flowers. *Liriodendron* (Tulip tree) N. America.

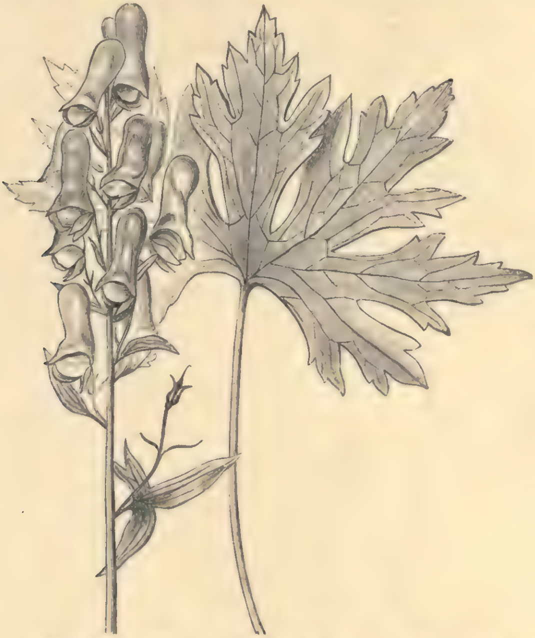


FIG. 596.—*Aconitum lycoctonum* (½ nat. size). *POISONOUS.*

OFFICIAL.—ANISI STELLATI FRUCTUS, Star-anise, is obtained from *Illicium anisatum* (China). The fruits of *Illicium religiosum* (Japan) are poisonous.

Family 4. **Anonaceae.**—Woody plants of tropical Asia and America. K 3, C 3 + 3, in other respects like the preceding families. Seeds with ruminated endosperm. Species of *Anona* yield succulent fruits. A perfume is obtained from *Cananga odorata.*

Family 5. **Myristicaceae** (21).—Tropical, woody plants. Diœcious. *Myristica fragrans* (Figs. 598, 599). The male and female flowers are similar in appearance and resemble those of the Lily of the Valley; perianth simple, trimerous.

Male flower with a central column around which 3-15 adherent anthers are arranged. Female flower with one ovule enclosed by the single carpel. Fruit berry-like, with coarse flesh, but dehiscent. Seed with ruminated endosperm and arillus.

OFFICIAL.—MYRISTICA, Nutmeg. The seed of *Myristica fragrans* divested of its testa.

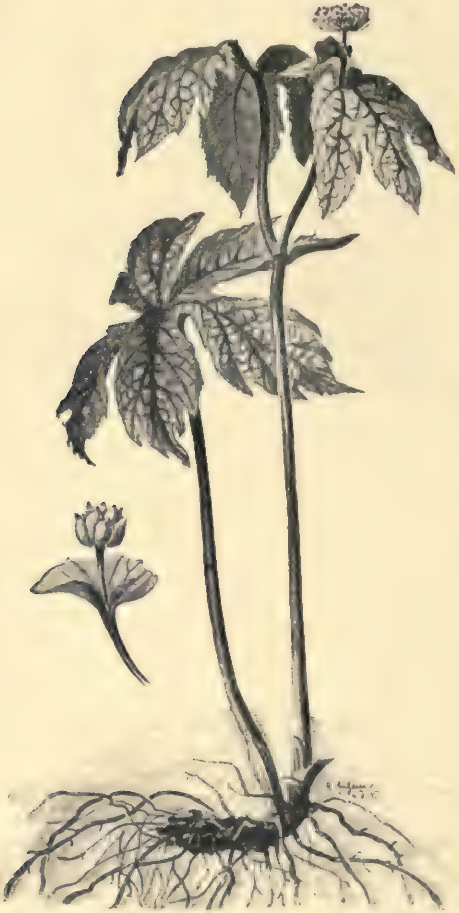


FIG. 597.—*Hydrastis canadensis* (½ nat. size). The apocarpous fruit to the left. *OFFICIAL.*

Family 6. **Berberidaceae.**—Flowers formed of a varying number of trimerous whorls. Carpel always solitary. K3+3, C3+3, A3+3, $\underline{G}1$. In *Berberis vulgaris* the leaves on the shoots of unlimited growth are transformed into spines; the short shoots bear simple leaves and terminate in racemes of flowers. The stamens are irritable to contact (cf. p. 296).

OFFICIAL. — PODOPHYLLI RHIZOMA obtained from *Podophyllum peltatum* (Fig. 600), a North American, herbaceous plant with large, palmately divided leaves and a terminal flower.

Family 7. **Menispermaceae.**—Similar to the preceding family but G3. For the most part tropical, climbing plants.

OFFICIAL. — CALUMBAE RADIX obtained from *Jatrorrhiza palmata* (Fig. 601) from Portuguese East Africa.

Family 8. **Lauraceae.**—Aromatic trees or shrubs with entire leathery leaves, which usually persist for several seasons. Only *Sassafras*, which has three-lobed leaves as well as simple ones, sheds its foliage annually. No stipules. Flowers inconspicuous, borne in panicle-like inflorescences. They are actinomorphic and composed of trimerous whorls. Androecium of four whorls, some of which frequently consist of staminodes or are wanting. Anthers opening by valves. Filaments sometimes bearing glands. Carpels 3, coherent

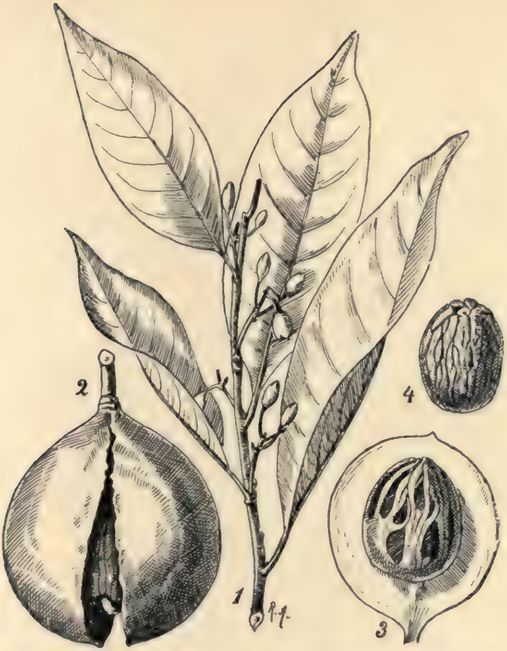


FIG. 598.—*Myristica fragrans.* *1*, Twig with male flowers (½ nat. size). *2*, Ripe pendulous fruit opening. *3*, Fruit after removal of one-half of the pericarp, showing the dark brown seed surrounded by the ruptured arillus. *4*, Kernel freed from the seed-coat. *OFFICIAL.*

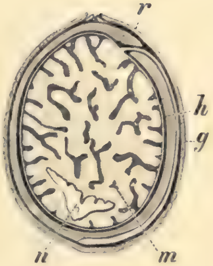


FIG. 599.—*Myristica fragrans*, seed, cut through longitudinally; *g*, aril; *h*, outer integument, interrupted at *r* by the raphe; *m*, ruminated endosperm; *n*, embryo (nat. size). *OFFICIAL.* (After BERG and SCHMIDT.)

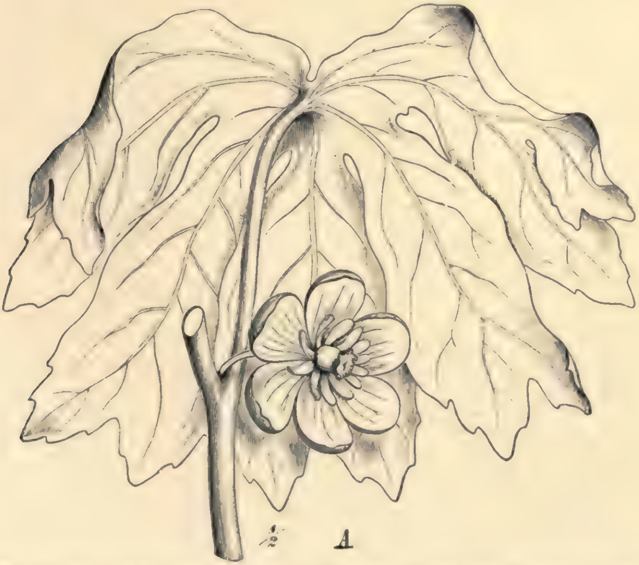


FIG. 600.—*Podophyllum peltatum* (½ nat. size). *OFFICIAL.* (From *Nat. Pflanzenfamilien*, iii.$_2$.)

to form an unilocular ovary with one, pendulous ovule. Fruit, a berry or drupe. Endosperm wanting. Floral formula, P 3 + 3, A 3 + 3 + 3 + 3, G $\underline{3}$ (Figs. 602, 603).

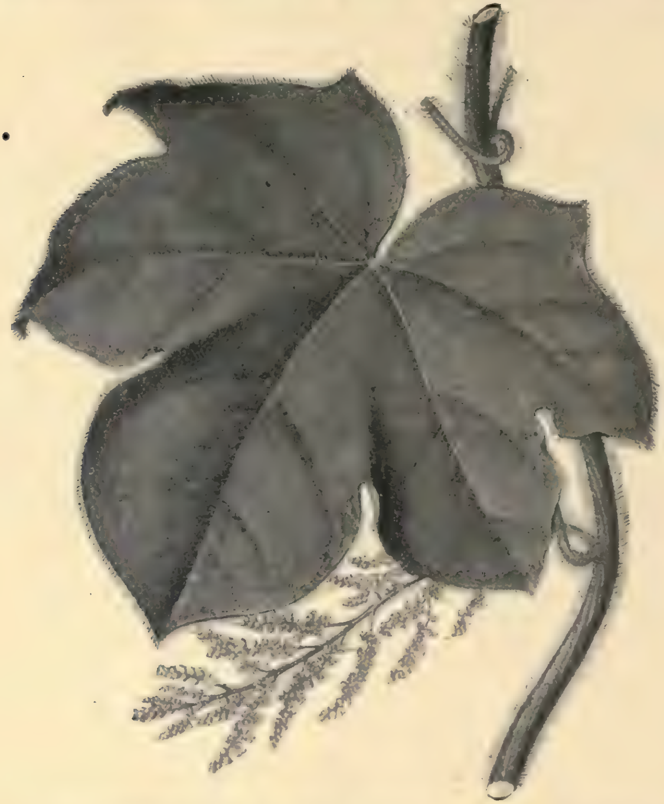


FIG. 601.—*Jatrorrhiza peltata* (½ nat. size). *OFFICIAL.* (After BERG and SCHMIDT.)

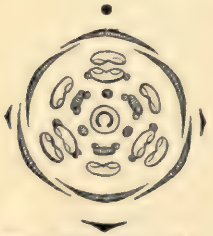


FIG. 602.—Floral diagram of *Persea*. (After EICHLER.)

IMPORTANT GENERA AND SPECIES ([22]).—*Laurus nobilis*, the Laurel, is a diœcious, evergreen tree of the Mediterranean region, which was well known in the early period of the Grecian civilisation; it is frequently grown in cool greenhouses (Fig. 604). Large plantations are grown at the Lake of Garda, where the oil is extracted, and here the trees ripen their oval, blackish-blue drupes in October. The widening of the floral axis just below the insertion of the fruit is characteristic. The genus *Cinnamomum* includes a number of economically important trees such as the Camphor tree from Japan and China (Fig. 605) and the Cinnamon tree from China and Ceylon. The latter is a stately evergreen with smooth, leathery leaves and inconspicuous, greenish flowers in axillary inflorescences. *Persea gratissima* (Fig. 602) is a native of tropical Mexico, and is frequently cultivated as a fruit tree in the tropics. Its fruit is known as the Avocado Pear. Species of *Cassytha*, the only genus of the family including herbaceous species, occur throughout the tropics as parasites resembling *Cuscuta*.

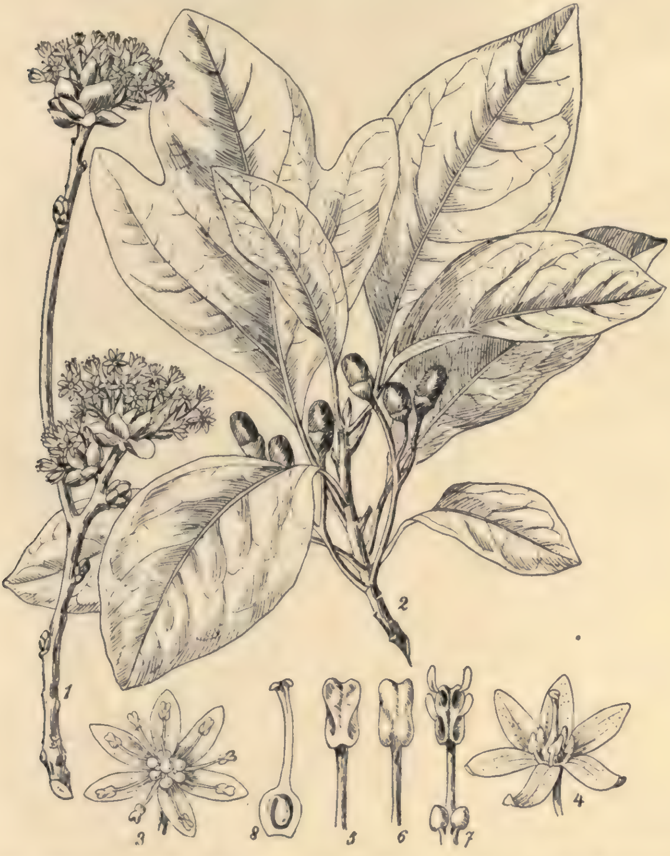


FIG. 603.—*Sassafras officinale*. (½ nat. size. After BERG and SCHMIDT.) *1*, Male inflorescences on a still leafless branch. *2*, Fruits on a leafy shoot. *3*, Male flower. *4*, Female flower. *5*, *6*, Closed stamens of the two outer whorls. *7*, Opened stamen of the innermost whorl. *8*, Ovary showing the style and the ovule. *OFFICIAL.*

OFFICIAL.—CAMPHORA, Camphor, is obtained from *Cinnamomum Camphora*. CINNAMOMI CORTEX and OLEUM CINNAMOMI from *Cinnamomum zeylanicum*. SASSAFRAS RADIX from *Sassafras officinale*, a diœcious, North American tree.

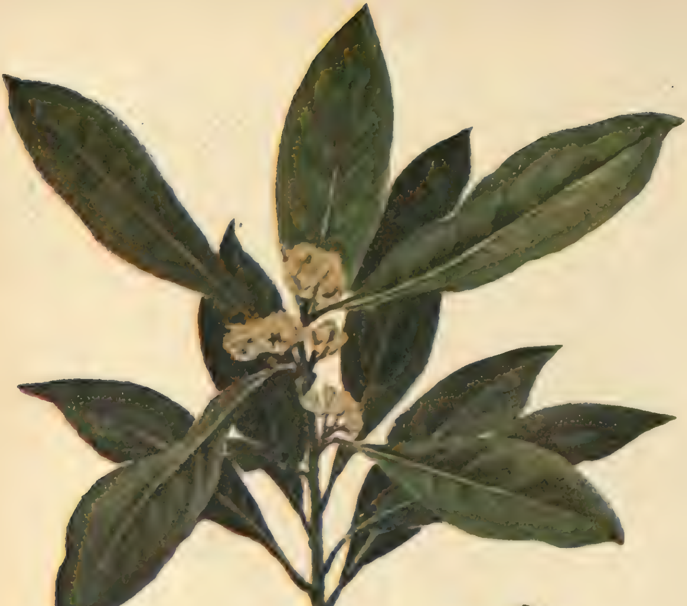


FIG. 604 A.—*Laurus nobilis* with male flowers. (½ nat. size.)

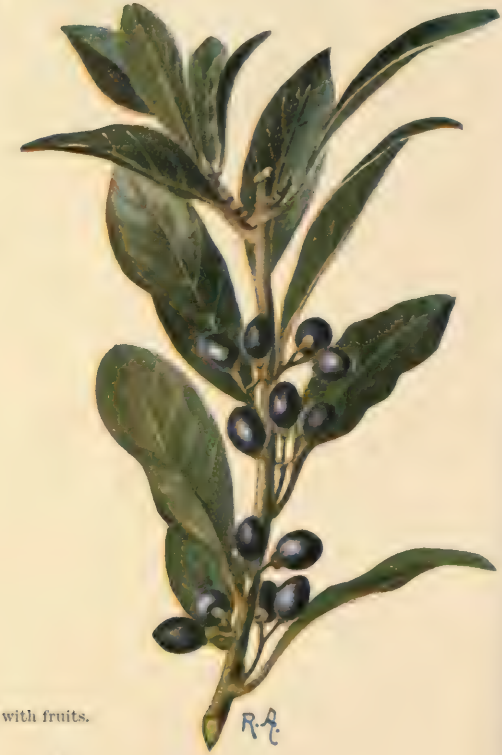


FIG. 604 B.—*Laurus nobilis* with fruits. (½ nat. size.)

MARINE BIOLOGICAL LABORATORY
WOODS HOLE
LIBRARY
MASS.

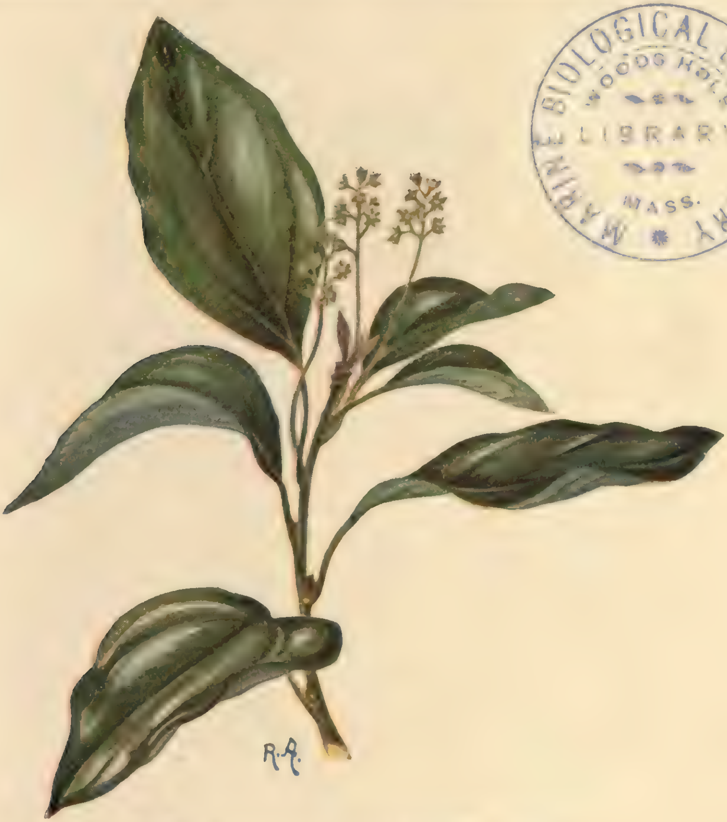


Fig. 605.—*Cinnamomum Camphora* (½ nat. size). *OFFICIAL.*

Order 8. Rhoeadinae

Herbs, or more rarely shrubs, with alternate, exstipulate leaves. Flowers hermaphrodite, cyclic; whorls usually bimerous. Ovary superior, unilocular. Placentas on the united margins of the carpels, projecting more or less into the cavity. Stigmas commisural, *i.e.* situated immediately over the sutures. Dehiscence of the fruit by separation of the middle portions of the carpels from the persistent placentas.

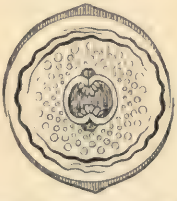


Fig. 606.—Floral diagram of *Glaucium.* (After Eichler.)

Family 1. **Papaveraceae.** — Herbs with milky juice. Leaves usually pinnately lobed. Flowers actinomorphic. Floral formula, $K\,2$, $C\,2+2$, $A\,\infty$, $G\,(2)$ or $\underline{\infty}$. Seeds with abundant endosperm (Fig. 606)..

The number of the stamens, and usually their position, is indefinite. In the genera *Chelidonium*, *Glaucium*, *Escholtzia*, there are two carpels; in *Papaver*, *Argemone*, and *Meconopsis* the number is greater (14-16).

IMPORTANT NATIVE GENERA.—*Chelidonium majus*, Celandine, has yellow latex and a bicarpellary ovary. A number of species of *Escholtzia*, *Argemone*, and *Papaver* are cultivated as ornamental plants. *Papaver Rhoeas*, the Poppy (Fig. 607), is a common weed in corn-fields or dry meadows. The leaves are narrow and pinnately divided. The whole plant is covered with coarse, bristly

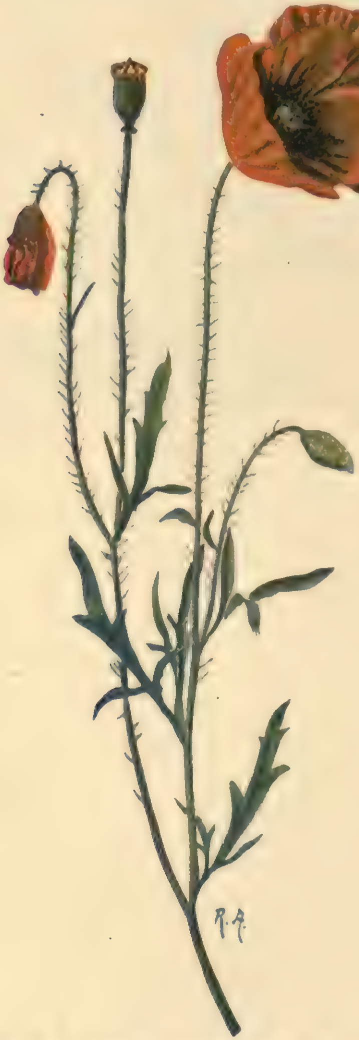


FIG. 607.—*Papaver Rhoeas* (½ nat. size). OFFICIAL.

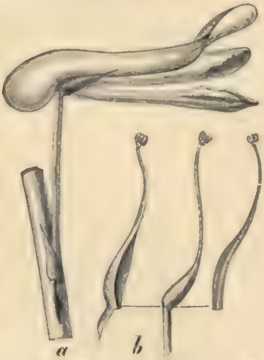


FIG. 608.—*Corydalis aurea.* *a*, Part of axis of raceme with a flower; *b*, style and stamens. (× 2.)

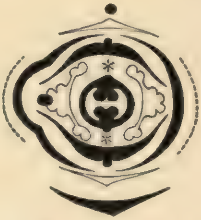


FIG. 609.—Floral diagram of *Corydalis cava.* (After EICHLER.) At the base of the stamen standing above the spur is a nectary.

hairs. The bent position of the flower bud is characteristic of many Papaveraceae. Ultimately the flower becomes erect as it opens; the two sepals forming the calyx are thrown off, and the four, large, wrinkled petals, forming the corolla, expand. *Papaver somniferum*, which is of oriental origin, has abundant, white latex. The plant has a glaucous bloom and, except on the flower-stalks, which bear a few bristly hairs, is glabrous. Leaves sessile, margin irregularly serrate or lobed. Petals violet or white with a dark patch at the base. Ovary unilocular, incompletely septate by the projection inwards of the numerous placentas. Fruit ripens erect on the peduncle. In *Papaver* the separation of the central portion of each carpel from the placentas at dehiscence is limited to the tips of the carpels. These bend outwards just below the flat stigmatic expansion, and the kidney-shaped seeds are thrown out of the small openings when the capsule borne on its long stalk is moved by the wind.

OFFICIAL.—*Papaver somniferum*, the Opium Poppy, yields PAPAVERIS CAPSULAE and OPIUM. *Papaver Rhoeas* yields RHOEADOS PETALA.

Family 2. **Fumariaceae.**—Glabrous herbs, without milky juice, with bipinnate or tripinnate leaves. Flowers bimerous throughout; the number of whorls in the corolla is doubled. Floral formula, K2, C2+2, A2, G(2). The outer petals, or one of them, bear spurs. In the latter case the flower is transversely zygomorphic (Figs. 608, 609). The inner whorl of stamens is suppressed. The stamens of the outer whorl are each tripartite, consisting of a central anther with two thecæ and two lateral anthers each with a single theca borne on a common filament. In *Hypecoum* the lateral branches join in pairs, and apparently form the inner staminal whorl, the position of which they occupy. The transversely zygomorphic flowers of the Fumariaceae with only one spur afford the only example of this type of symmetry. The fruits of *Fumaria* are nutlets, those of *Corydalis* and *Dicentra* are capsules. *Dicentra spectabilis*, which is frequently cultivated, has a bisymmetrical corolla with two spurs. Seeds with endosperm.

Family 3. **Cruciferae** (23). Annual, biennial, or perennial herbs without milky juice. Inflorescence racemose, usually without bracts or bracteoles. Flowers actinomorphic, always lateral, composed of bimerous whorls. Floral formula, K 2 + 2, C 2 + 2, A 2 + 4, G (2). The outer whorl of sepals stands in the median plane; the four petals alternate with the sepals. The two outer stamens are shorter than the four inner ones which stand in the median plane. The latter correspond to two stamens branched to the base. The carpels form a superior, usually pod-like, ovary, which is divided into two chambers by a false septum stretching between the parietal placentas. The fruit opens by the separation from below upwards of the main portion of each carpel, leaving the seeds attached by their stalks to the central portion formed by the placentas together with the false septum. Rarely the fruit is indehiscent. Embryo curved. Endosperm wanting or reduced to a single layer of cells coherent with the seed coat (Figs. 610-616).

The form of the fruit and the position of the embryo in the seed are used in the subdivision of this extremely uniform family. This general classification, which dates from the time of Linnaeus, will be used here, but reference must be made to the more recent, natural division of the family, founded on characters afforded by

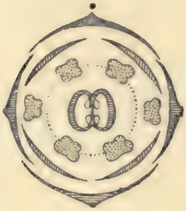


FIG. 610. Cruciferae. Floral diagram (*Brassica*).

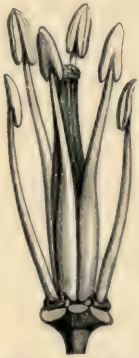


FIG. 611.—*Cardamine pratensis.* Flower with perianth removed. (After BAILLON, × 4.)

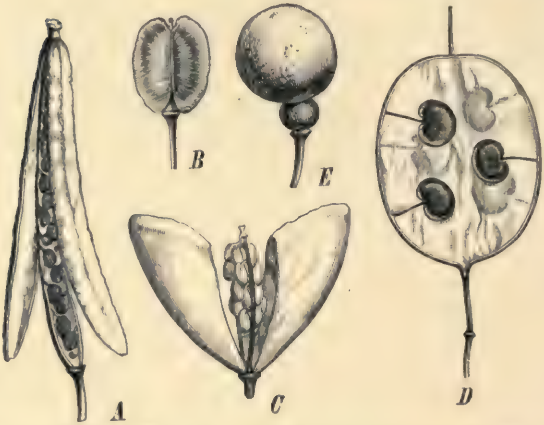


FIG. 612.—Cruciferous fruits. *A*, *Cheiranthus cheiri* ; *B*, *Lepidium sativum* ; *C*, *Capsella bursa pastoris* ; *D*, *Lunaria biennis*, showing the septum after the carpels have fallen away. *E*, *Crambe maritima*. (After BAILLON.)

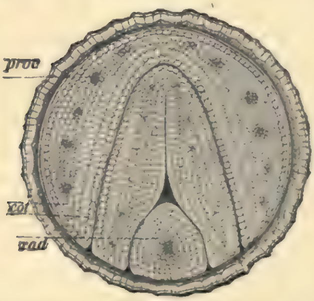


FIG. 613.—Transverse section of the seed of *Brassica nigra*. *rad*, radicle ; *cot*, cotyledons ; *proc*, vascular bundles. (After MOLLER.)

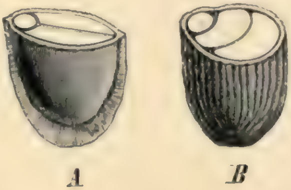


FIG. 614.—Seeds of Cruciferae cut across to show the radicle and cotyledons. *A*, *Cheiranthus cheiri* (× 8) ; *B*, *Sisymbrium alliaria* (× 7). (After BAILLON.)

a number of organs, which is given in the *Natürlichen Pflanzenfamilien* by PRANTL. LINNÆUS distinguished the *Siliquosae*, in which the fruit is a siliqua, from the *Siliculosae*, in which it is a short silicula. The Siliquosae are further divided into *Siliquosae dehiscentes*, with the usual type of siliqua, and *Siliquosae lomentaceae*, in which the siliqua breaks transversely into one-seeded joints. The Siliculosae are also divided into *Siliculosae dehiscentes* and *Siliculosae nucamentaceae* with indehiscent fruits. The Siliculosae dehiscentes were later divided by A. P. DE CANDOLLE into the *S. latiseptae* with a broad septum and the *S. angustiseptae* in which the septum is narrow.

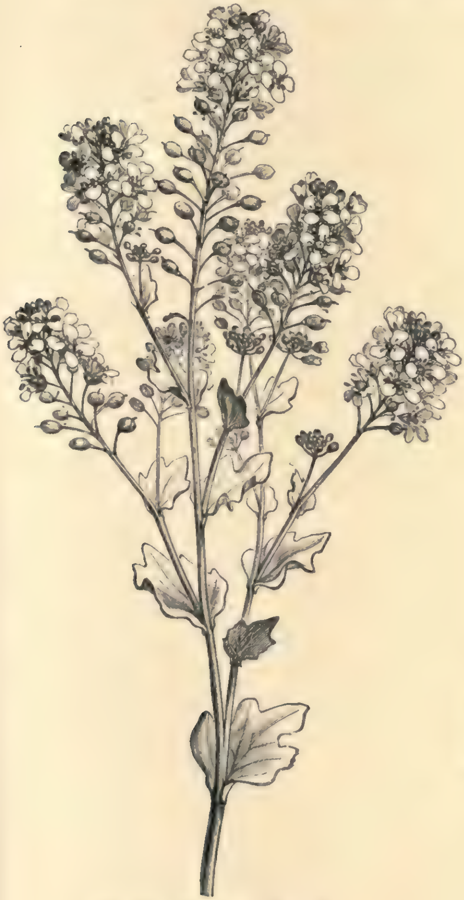


FIG. 615.—*Cochlearia officinalis.* (After BAILLON.)

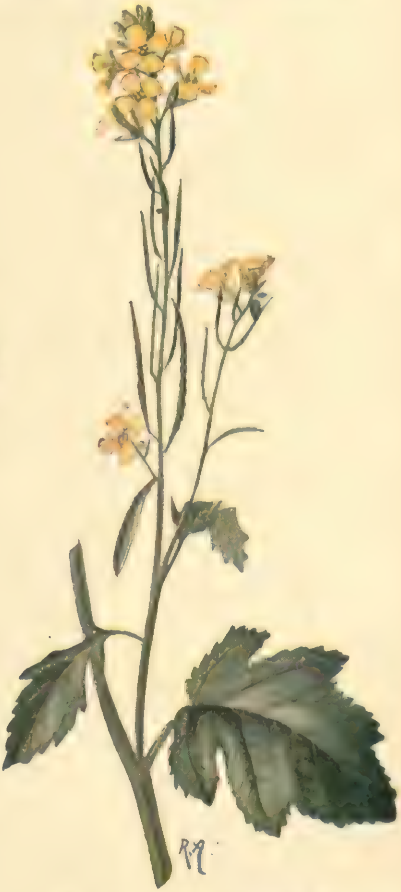


FIG. 616.—*Brassica nigra* (½ nat. size). *OFFICIAL.*

The number of species and their abundance make the Cruciferae one of our most important, native families of flowering plants. Their brightly coloured, mostly yellow flowers render them conspicuous in various situations and at all periods of the year. The nectaries, which are borne on the receptacle at the base of the stamens, also show that the flowers are entomophilous. The family includes a number of economic plants.

1. *Siliquosae dehiscentes: Cheiranthus Cheiri*, the Wallflower (Figs. 612 *A*, 614 *A*). *Matthiola*, the Stock. Numerous species of *Brassica* have been long in cultivation: *B. oleracea*, the Wild Cabbage, in its various forms—(*a*) *sylvestris*, which occurs on the coasts of Northern Europe and is to be regarded as the wild form: (*b*) *acephala*, Borecole or Kale; (*c*) *gongylodes*, Turnip-rooted Cabbage; (*d*) *gemmifera*, Brussels Sprouts; (*e*) *sabauda*, Savoys; (*f*) *capitata*, the Cabbage; (*g*) *Botrytis*, Cauliflower and Broccoli. *Brassica campestris*, with the cultivated forms—(*a*) *annua*, (*b*) *oleifera*, (*c*) *rapifera*. *Brassica napus*, the Turnip—(*a*) *annua*, (*b*) *oleifera*, (*c*) *napibrassica*. *Brassica nigra*, Black Mustard (Figs. 613-616), an annual plant derived from the eastern Mediterranean region, was cultivated even in ancient times. The radical leaves are long-stalked and lyrate with rounded terminal lobes; on ascending the copiously branched stem they become lanceolate and gradually smaller. The plant is glabrous except for some bristly hairs on the upper surface of the leaf. Inflorescence a raceme; the bright yellow flowers stand out from the main axis, while the developing fruits are erect and applied to the axis. The mature fruits have a short beak; the slightly convex valves are keeled and traversed by a well-marked midrib. Seeds spherical. *Sinapis alba*, White Mustard, is a hairy plant, distinguishable from the Black Mustard by the long broadly-beaked fruits, the valves of which bear coarse bristly hairs. The fruits project from the axis of the inflorescence. The seeds are yellowish-white and twice as large as those of *Brassica nigra*.

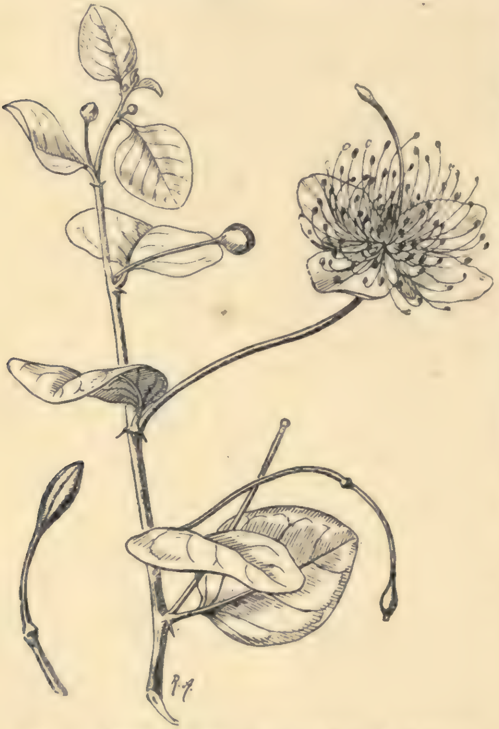


FIG. 617.—*Capparis spinosa*. Flowering branch and a young fruit borne on the gynophore. (½ nat. size.)

2. *Siliquosae lomentaceae*: *Crambe* (Fig. 612 *E*), with the lower portion of the siliqua sterile, and *Cakile* are thick-leaved, strand plants. *Raphanus sativus*, the Radish.

3. *Siliculosae dehiscentes latiseptae*: *Vesicaria*, *Aubrietia*, *Draba*, *Lunaria*,

(Fig. 612 *D*). *Cochlearia officinalis*, Scurvy Grass (Fig. 615), is a glabrous, biennial herb which germinates in summer, forming a large rosette of stalked, cordate leaves, persists over winter, and early in the succeeding summer produces a low, copiously branched inflorescence of white flowers. The rosette of radical leaves has disappeared by the time the fruit is ripe.

4. *Siliculosae dehiscentes angustiseptae*: *Thlaspi*, *Iberis* with somewhat zygomorphic flowers, *Capsella* (Fig. 612 *C*).

5. *Siliculosae nucamentaceae*: *Isatis tinctoria*, Woad.

OFFICIAL.—SINAPIS ALBAE SEMINA, from *Sinapis alba*; SINAPIS NIGRAE SEMINA, from *Brassica nigra*. ARMORACIAE RADIX, from *Cochlearia Armoracia*.

Family 4. **Capparidaceae.**—Herbs or shrubs with simple or palmately-divided leaves, often stipulate. Flowers as in the Cruciferae, $K4$, $C4$, $A2+2$, $G(\underline{2})$; they differ by the intercalation of a gynophore raising the ovary high above the level of the other parts of the flower, and by the branching of the stamens (or some of them) giving rise to an indefinite number (Fig. 617). Fruit usually a berry, in other cases a capsule or drupe. Seeds without endosperm.

Capparis spinosa is a small shrub occurring on rocky ground in the Mediterranean region. The leaves are simple with short, recurved, spiny stipules. The actinomorphic flowers are axillary and solitary; the androecium by chorisis consists of numerous members. The fruit is a berry which reaches the size of a plum and contains numerous seeds. Capers are prepared from the young flower buds.

Family 5. **Resedaceae.**—Herbs with alternate leaves and zygomorphic flowers forming a dense raceme. The sexual organs are borne on a gynophore or disc. $K5\text{-}8$, $C5\text{-}8$, $A\,\infty$, $G(\underline{2\text{-}6})$. The ovary is unilocular and open above, or the carpels are free. *Reseda odorata*, Mignonette. *R. lutea*, *R. luteola*, British.

Order 9. Insectivorae (24)

This small order includes the three families of the **Sarraceniaceae**, **Nepenthaceae**, and **Droseraceae**, which were formerly placed in the Cistifloræ. The name has reference to the capacity for capturing and digesting insects which is shown by many representatives of these families (cf. p. 236, Figs. 208-210). The common affinity of the three families is now generally admitted, and they may perhaps be connected on to the Resedaceae.

Genera of Sarraceniaceae: *Sarracenia*, *Darlingtonia*, North American, marsh- and moor-plants.

Genus of the Nepenthaceae: *Nepenthes*, diœcious, climbing, pitcher-plants of tropical Asia (Fig. 46).

Genera of the Droseraceae: *Dionaea*, Venus' Fly-trap, North America. *Aldrovanda vesiculosa*, a European Water-plant, also found in India and Australia. *Drosera*, the Sundew; many species occur on peat-moors. *Drosophyllum lusitanicum*, Spain and Portugal.

Order 10. Saxifraginae

Herbs or woody plants of very diverse habit, with actinomorphic, pentamerous flowers. Androecium usually obdiplostemonous. Carpels 2-5, free or coherent. Flowers hypogynous, perigynous or epigynous.

The family of the **Podostemonaceae** (24a) may be included in this order. The vegetative and reproductive organs of these plants are peculiarly modified in relation to their mode of life, and the situations they occupy in the most rapid currents and waterfalls of rivers and streams in the tropics.

Family 1. **Crassulaceae.**—Succulent (25) herbs or under-shrubs with cymose inflorescences. Flowers hermaphrodite, with calyx and corolla consisting of a variable number of members. Obdiplostemonous or haplostemonous. Carpels free (Fig. 618) flower hypogynous or perigynous. Scale-like nectaries at the base of the carpels. Fruit a capsule containing numerous seeds with a small amount of endosperm.

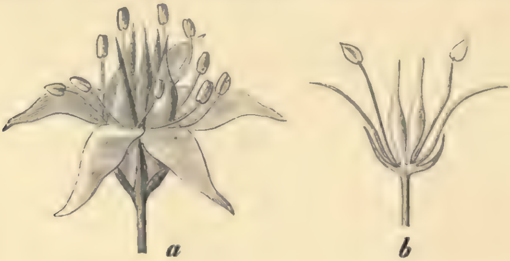


FIG. 618.—*Sedum Telephium.* *a*, Flower; *b*, flower in longitudinal section. (× 4.)

MORE IMPORTANT GENERA.—*Sedum* with pentamerous flowers; there are a number of British species. *Sempervivum*, flowers with from six to an indefinite number of whorls; *S. tectorum*. *Bryophyllum* with tetramerous flowers, noteworthy on account of the abundant formation of buds in the indentations of the margin of the leaf. *Crassula*.

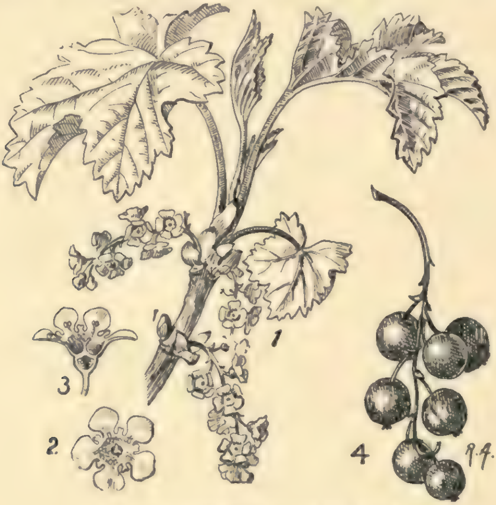


FIG. 619.—*Ribes rubrum.* ($\frac{2}{3}$ nat. size.)

Family 2. **Saxifragaceae** (26).—Herbs or woody plants with alternate leaves. Flowers hermaphrodite, obdiplostemonous, tetramerous or pentamerous, perigynous or epigynous. Carpels usually two; ovary uni- or bi-locular. Fruit a capsule or a berry containing an indefinite number of albuminous seeds.

IMPORTANT GENERA.—*Saxifraga*, Saxifrage, small herbaceous plants which are especially numerous on crags and rocky ground in mountainous districts. They have a rosette of radical leaves (cf. p. 211, chalk glands) and bear numerous pentamerous flowers grouped in various types of inflorescence. The two partially inferior carpels are distinct from one another above. *Parnassia palustris* is common on wet moors, K5, C5, A5+5, G(4). Ovary unilocular, placentation parietal. One whorl of stamens modified into palmately divided staminodes, which serve as nectaries. *Cephalotus follicularis* is an Australian, insectivorous plant, and possesses, in addition to the ordinary leaves with a flat, elliptical lamina, others metamorphosed into pitchers. The species of *Ribes* have an inferior ovary which develops into a berry, and on this account are commonly cultivated. *R. rubrum* (Fig. 619), Red Currant, *R. nigrum*, Black Currant, *R. grossularia*, Gooseberry. Other Saxifragaceae are favourite ornamental plants, *e.g.* *Ribes aureum* and *R. sanguineum*, *Hydrangea*, *Philadelphus*, and *Deutzia*.

Family 3. **Hamamelidaceae.**—Woody plants of the tropics and sub-tropics. *Liquidambar* is monœcious. Flowers in heads; male flowers apetalous, with an indefinite number of stamens; female flowers with a perianth and a bilocular ovary. *Liquidambar styraciflua* is a common tree in North American forests.

OFFICIAL.—STYRAX PRAEPARATUS from *Liquidambar orientalis*. HAMAMELIDIS CORTEX and FOLIA from *Hamamelis virginiana*.

Family 4. **Platanaceae.**—Stately trees with alternate, three- to five-lobed leaves and large stipules. Flowers diclinous, monœcious, in small spherical heads, three or four of which are borne at some distance from one another on pendulous stalks. Male flowers with three to four stamens; female flowers with four free carpels. Perianth inconspicuous.

Species of *Platanus* are commonly planted as shade trees by the sides of the streets.

Order 11. Rosiflorae

Family **Rosaceae** (27).—This is the only family in the order. Herbs, shrubs, and trees with alternate, stipulate leaves, showing considerable differences in form and habit. Flowers nearly always actinomorphic, with the members in whorls. K 5, C 5. Stamens usually numerous. Flowers perigynous or epigynous; one to many free carpels borne on the expanded, convex or hollowed floral axis. In the epigynous flowers only the styles are free. The floral axis in many cases takes part in the construction of the fruit. Seeds usually without endosperm.

The apocarpous pistil and numerous stamens are characteristic of the Rosaceae (Fig. 620). Both these features are also found in the Ranunculaceae or generally in the Polycarpicae, but the floral members are there spirally arranged while in the Rosaceae they are in whorls. The latter are further distinguished by the peculiar development of the floral axis (Fig. 621). In many cases the increase in number of members of the androecium and gynaeceum proceeds from an intercalary zone of the hollowed floral axis, and continues for a considerable period. The introduction of new members is determined by the spatial relations, so that differences in the numbers of members are found in individuals of the same species.

The family is divided into a number of sub-families.

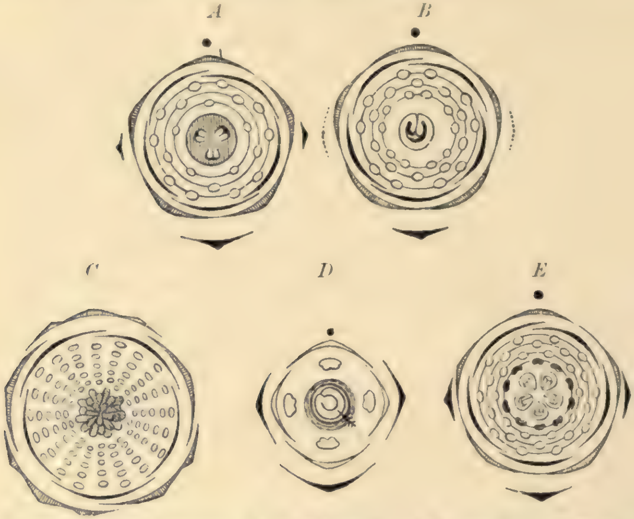


FIG. 620.—Floral diagrams of Rosaceae. *A*, *Sorbus domestica*; *B*, *Prunus Padus*; *C*, *Rosa tomentosa*; *D*, *Sanguisorba officinalis*; *E*, *Spiraea hypericifolia*. (After EICHLER.)

(*a*) *Spiraeeae.* K 5, C 5, A 5 + 5 or more, G 5; other numbers of members in the whorl are less frequent. Carpels free or united, each containing two or more ovules. Fruits usually dehiscent. Floral axis expanded as a more or less flat disc. The genus *Spiraea* has inflorescences bearing numerous flowers; many species are cultivated as ornamental shrubs (Fig. 620 E). *Quillaja Saponaria* (Fig. 622), from Chili, is an evergreen tree with shortly stalked, alternate, leathery leaves and terminal dichasia usually consisting of three flowers. The flower has a five-toothed, nectar-secreting disc projecting above the large sepals. Five of the stamens stand at the projecting angles of the disc opposite the sepals; the other five are inserted

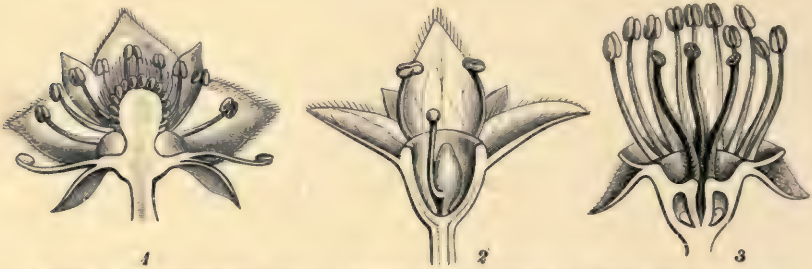


FIG. 621.—Rosaceae. Three flowers cut through longitudinally to show different forms of the receptacle. *1*, *Potentilla palustris*; *2*, *Alchemilla alpina*; *3*, *Pyrus malus*. (After FOCKE in *Naturl. Pflanzenfamilien*.)

opposite the petals at the inner margin of the disc. Petals narrow, white. Ovary superior. Only the middle flower of the dichasium is hermaphrodite and fertile, the lateral flowers are male and have a reduced gynaeceum. Fruit star-shaped, composed of partial fruits. Each carpel dehisces by splitting into two valves. Seeds winged.

(*b*) *Pomeae.*—These are distinguished from the other Rosaceae by their inferior ovary, which usually consists of five carpels bound together by the hollow floral receptacle so that only the styles are free. Each carpel contains one to many ovules. The fruit resembles a berry, the floral receptacle becoming succulent. The boundaries of the separate loculi are formed of parchment-like or stony tissue. The seeds are exalbuminous and enclose a well-developed embryo with fleshy cotyledons. *Pyrus malus*, Apple (Fig. 621, 3 ; Fig. 623) and *P. communis*, the Pear, are important and long-cultivated fruit trees, of which numerous varieties are grown. *Cydonia vulgaris*, the Quince, has large, solitary, rose-coloured flowers. The fruits are in shape like an apple or pear, covered with fine woolly hairs and with a pleasant scent, though not edible when uncooked. In *Mespilus germanica*, the Medlar, the fruit has an apical depression surrounded by the remains of the calyx. The evergreen *Eriobotrya japonica*, is commonly planted in the Mediterranean region ; fruits contain several large seeds, and are succulent, having an acid flavour. *Sorbus* (*Pyrus*) *aucuparia*, the Rowan. *Crataegus* (*Mespilus*) *oxycantha*, the Hawthorn, in hedges or planted as an ornamental tree.

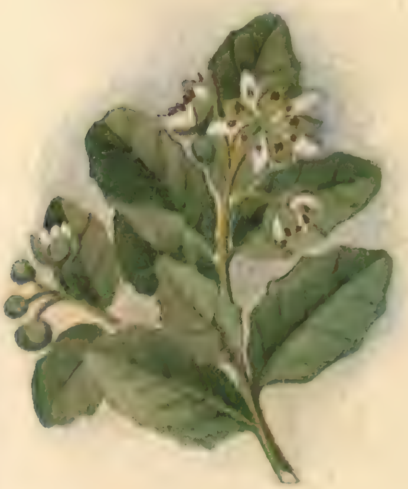


FIG. 622. *Quillaja Saponaria.* (½ nat. size. After A. MEYER and SCHUMANN.)

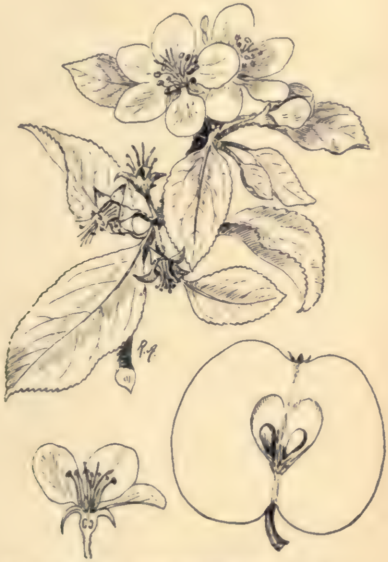


FIG. 623.—*Pyrus malus.* Flowering shoot, single flower, and fruit in longitudinal section. (½ nat. size.)

(*c*) *Roseae.*—Floral axis concave, pitcher-shaped, with one to many free carpels, each of which encloses 1-2 ovules. The partial fruits are nut-like, and are enclosed by the hollowed floral axis. *Rosa* with numerous species, varieties and cultivated forms, which have been for long valued on account of their form, colour, and scent (Fig. 620 C). The floral receptacle becomes succulent. Shrubs, some-

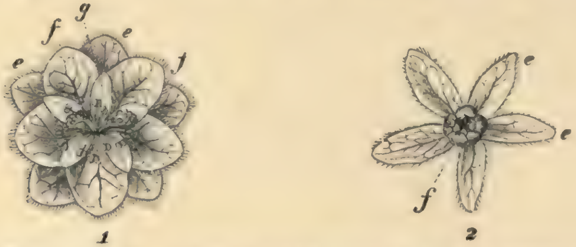


FIG. 624.—*Hagenia abyssinica.* 1, Female flower; *e*, epicalyx; *f*, calyx; *g*, corolla (× 4); 2, fruit (nat. size), with enlarged epicalyx. (After BERG and SCHMIDT.) *OFFICIAL.*

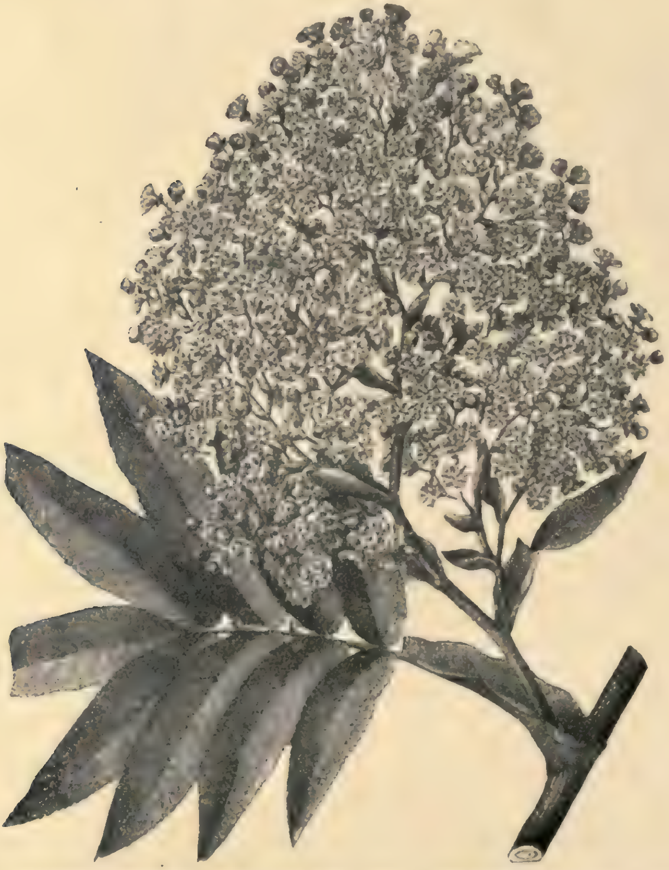


FIG. 625.—*Hagenia abyssinica.* Inflorescence (½ nat. size). (After BERG and SCHMIDT.) *OFFICIAL.*

times straggling climbers, with unequally pinnate leaves, the large stipules of which are adherent to the base of the leaf-stalk, and brightly coloured, conspicuous flowers. Sepals, inserted on the margin of the receptacle, leafy and pinnately divided (cf. Fig. 511). The double flowers result from the petaloid development of many of the stamens. *Agrimonia* and *Hagenia abyssinica* have a dry cup-shaped receptacle. *Hagenia* is a diœcious tree with unequally pinnate leaves, the adherent stipules of which render the petiole winged and channelled. Inflorescence a copiously branched panicle. Each flower has two bracteoles and an epicalyx. The flowers are unisexual by suppression of the male and female organs respectively. The corolla later falls off and the sepals become inrolled, while the epicalyx enlarges. The two free carpels have each a single ovule. Fruit one-seeded (Figs. 624, 625). *Alchemilla* has no petals ; the lack of a conspicuous corolla may perhaps stand in relation to the apogamous development of the embryo (11a) (Fig. 621, 2). *Sanguisorba officinalis* has polygamous flowers (cf. p. 541), without epicalyx or corolla, aggregated in heads. Flowers tetramerous with 1-2 carpels (Fig. 620 *D*).

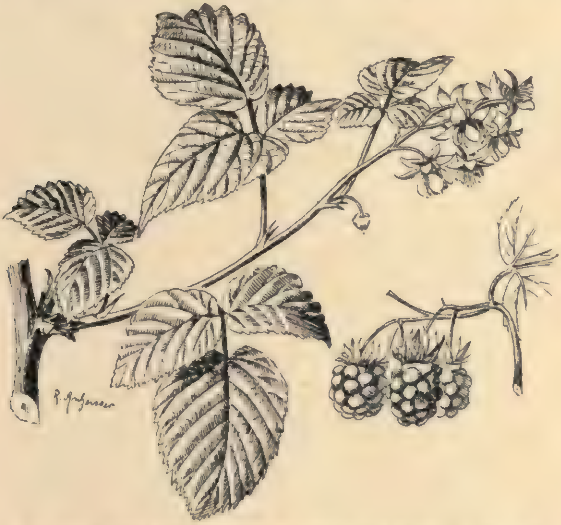


FIG. 626.—*Rubus idaeus*. Flowering branch and fruits. (½ nat. size.)

(*d*) *Potentilleae*.—Floral receptacle plate-shaped, flat or convex and bearing numerous free carpels which develop into nutlets, drupes, or berries. Each carpel with one ovule. Epicalyx often present. *Potentilla* with a number of British species (Fig. 621, 1). *Geum* and *Dryas* have hairy carpels which elongate in fruit and are distributed by the wind. The latter genus includes arctic and alpine forms. *Fragraria*, Strawberry, with small achenes situated on the succulent, enlarged, floral receptacle. *Rubus*, Blackberry, has numerous species, mostly scrambling shrubs with recurved prickles. Leaves trifoliate. *R. idaeus*, the Raspberry, is one of the few species which are not straggling climbers (Fig. 626). The small drupes are closely crowded on the convex receptacle, only slightly connected with one another. The withered style is for a long time visible on the partial fruits. *R. fruticosus*.

(*e*) *Pruneae.*—Flower perigynous, with a single carpel seated on the cup-shaped receptacle (Fig. 620 B). Ovules two. Fruit, a one-seeded drupe. The group includes a number of important fruit trees. *Prunus cerasus*, the Wild Cherry (Fig. 627); *P. avium*, Gean; *P. domestica*, the Plum; *P. armeniaca*, the Apricot, and *P. persica*, the Peach, are of Chinese origin; *P. Amygdalus*, the Almond, from the eastern Mediterranean region. The two last-named species have hairy fruits.

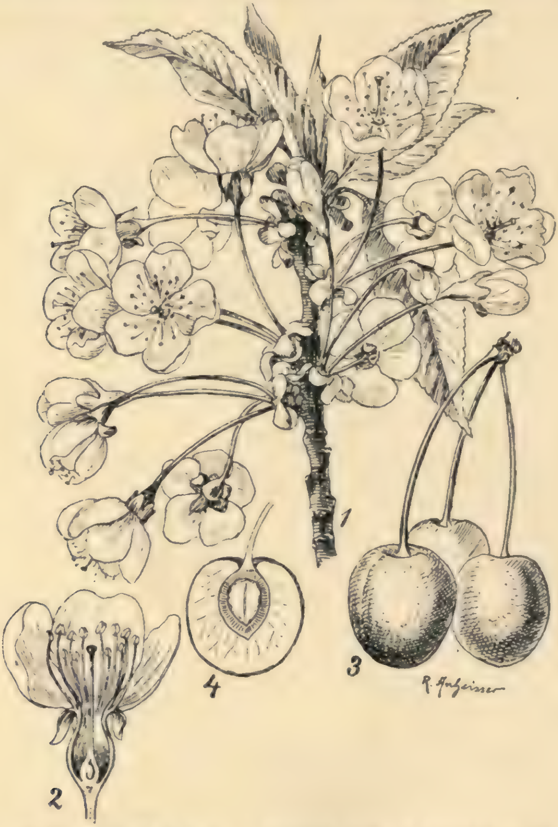


FIG. 627.—*Prunus cerasus* (⅔ nat. size). *1*, Flowering shoot; *2*, flower cut in two (slightly enlarged); *3*, fruits; *4*, fruit cut through longitudinally.

The succulent mesocarp of the Almond dries up as the fruit ripens, and ruptures, setting the stony endocarp free.

(*f*) *Chrysobalaneae.*—Frequently with dorsiventral flowers. A single carpel.

POISONOUS.—The seeds of many Rosaceae contain amygdalin, but usually not in such amount as to be poisonous, owing to the resulting hydrocyanic acid, when eaten fresh in small quantity; this is, however, often the case with the residuum left after the seeds, *e.g.* of bitter almonds, have been crushed. The leaves of the Cherry Laurel (*Prunus laurocerasus*) may also give rise to toxic effects.

OFFICIAL.—ROSAE GALLICAE PETALA from cultivated plants of *Rosa gallica*;

OLEUM ROSAE and AQUA ROSAE from *Rosa damascena.* AMYGDALA DULCIS and AMYGDALA AMARA from *Prunus amygdalus.* PRUNUM from *Prunus domesticus.* PRUNI VIRGINIANAE CORTEX from *Prunus serotina.* LAUROCERASI FOLIA from *Prunus laurocerasus.* CUSSO from *Hagenia abyssinica.* QUILLAIAE CORTEX from *Quillaja Saponaria.*

Order 12. Leguminosae (28)

The common characteristic of all Leguminosae is afforded by the pistil. This is always formed of a single carpel, the ventral suture of which is directed to the dorsal side of the flower (Figs. 628, 631, 637). It is unilocular and bears the ovules in one or two rows on the ventral suture. The fruit is usually a pod (legume), which dehisces by splitting along both the ventral and dorsal sutures (Fig. 642). Nearly all Leguminosae have alternate, compound, stipulate leaves. Many are provided with pulvini (Figs. 236, 237), which effect variation movements of the leaves and leaflets.

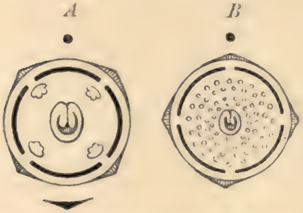


FIG. 628.—Floral diagrams of Mimosaceae. *A*, *Mimosa pudica*; *B*, *Acacia lophantha.* (After EICHLER.)

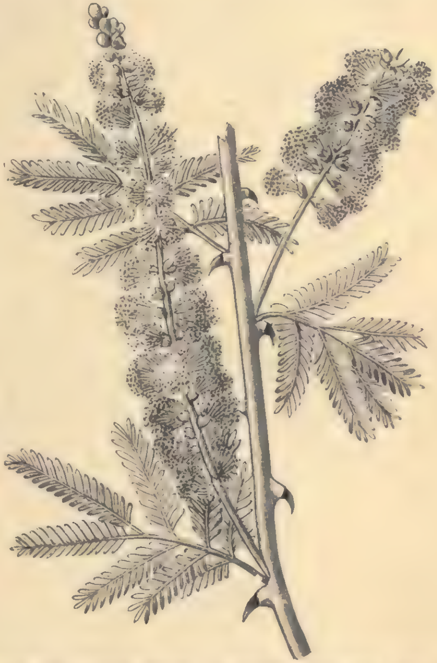


FIG. 629.—*Acacia senegal.* Flowering branch (nat. size). (After A. MEYER and SCHUMANN). *OFFICIAL.*

Family 1. **Mimosaceae.**—Trees, and erect or climbing, shrubby plants with bipinnate leaves. Flowers actinomorphic, pentamerous or tetramerous. Æstivation of sepals and petals valvate. Stamens free, numerous, or equal or double in number to the petals. The colour of the flower is due to the length and number of the stamens, the corolla being as a rule inconspicuous. The pollen grains are often united in tetrads or in larger numbers. The flowers are grouped in spikes or heads. Embryo straight in the seed.

IMPORTANT GENERA.—There are no representatives native to Europe. The Sensitive Plant (*Mimosa pudica*) (Fig. 237) occurs as a weed throughout the tropics and exhibits great irritability to contact (cf. p. 295). Numerous species of the genus *Acacia* are distributed through the tropics and sub-tropics of the old and new worlds; some are in cultivation in the Mediterranean region. The Australian forms of the genus are frequently characterised by possessing phyllodes (Figs.

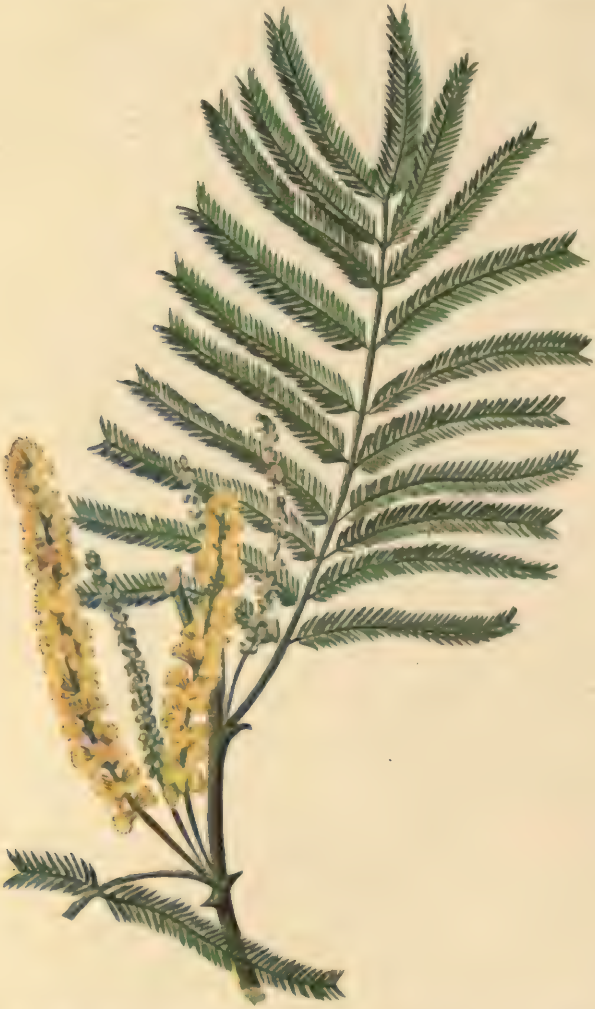


FIG. 630.—*Acacia Catechu.* (⅔ nat. size. After MEYER and SCHUMANN.)

171, 194), the vertical position of which contributes to the peculiar habit of the Australian forests. Only the seedlings of these species have a few bipinnate leaves which constantly succeed the cotyledons. Some American species of *Acacia* are inhabited by ants (cf. p. 235, Fig. 205) which live in the large stipular thorns and obtain food from Belt's food-bodies at the tips of the pinnules. The plants in this way are protected against the attacks of leaf-cutting ants. Many species of *Acacia* are of considerable economic value owing to the presence of gums and tannins

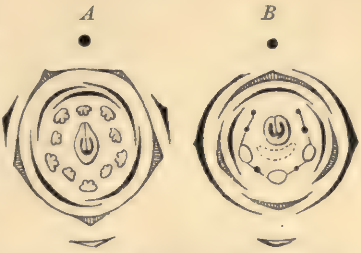


FIG. 631.—Floral diagrams of Caesalpiniaceae. *A*, *Cercis siliquastrum*; *B*, *Tamarindus indica*. (After EICHLER.)

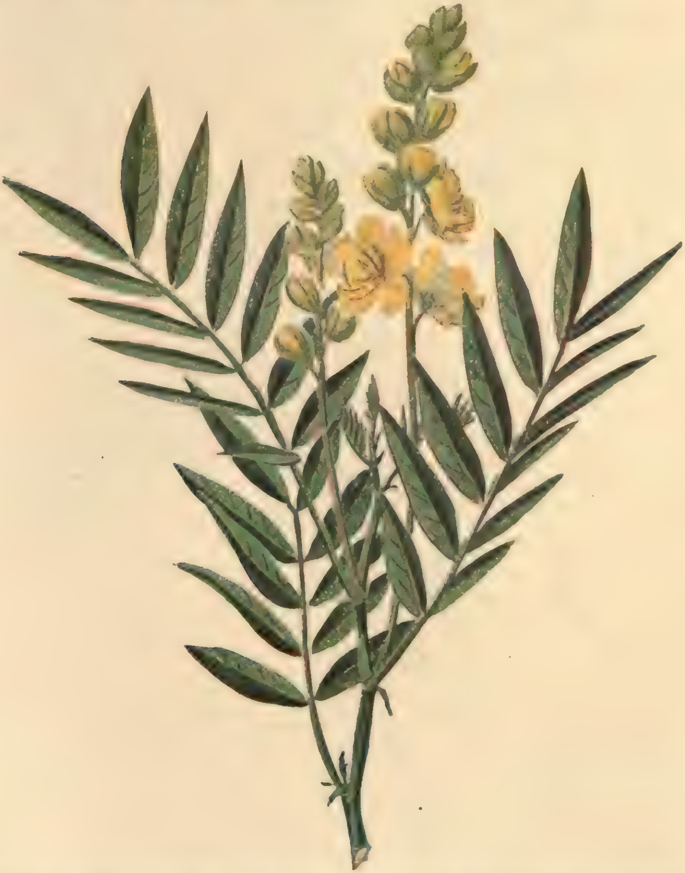


FIG. 632.—*Cassia angustifolia*. (⅔ nat. size. After A. MEYER and SCHUMANN.) *OFFICIAL.*

in the cortex or in the heart-wood. *A. catechu* (Fig. 630) and *A. suma* are East Indian trees from which Catechu is obtained.

OFFICIAL.—By the disorganisation of the parenchyma of the stem of *Acacia senegal* (Soudan and Senegambia) and of other species, ACACIAE GUMMI is obtained. This exudes from wounds as a thick fluid and hardens in the air.

Family 2. **Caesalpiniaceae.**—Trees or shrubs with pinnate or bipinnate leaves. Flowers usually somewhat dorsiventral. Corolla with ascending imbricate æstivation (Fig. 631) or wanting. Typical floral formula: K 5, C 5, A 5 + 5, $G\,\underline{1}$. The number of petals and stamens is often incomplete. Embryo straight.

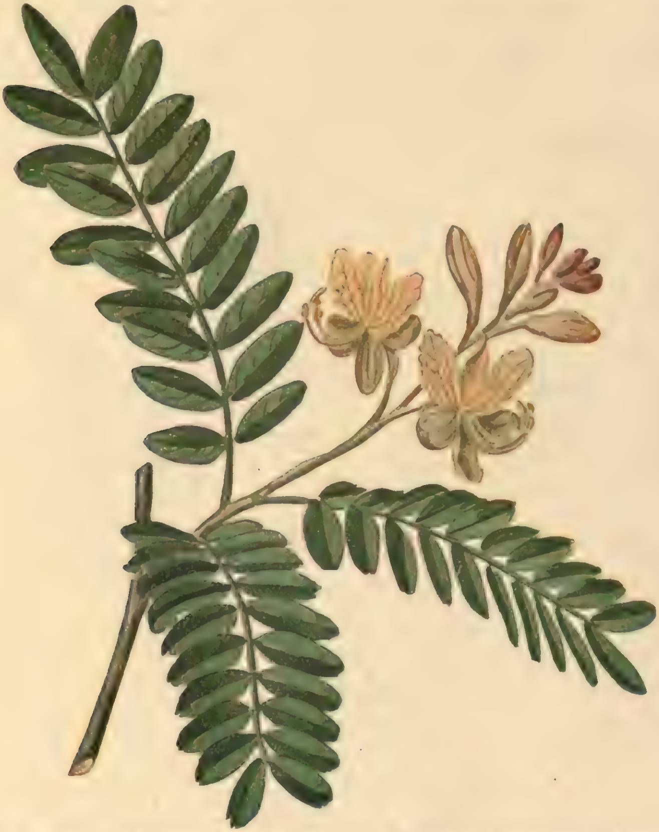


FIG. 633.—*Tamarindus indica*. (⅓ nat. size. After A. MEYER and SCHUMANN.) *OFFICIAL.*

IMPORTANT GENERA.—Characteristic examples of the Caesalpiniaceae are afforded by the flowers of *Cassia*. In the sub-group *Senna*, to which *C. angustifolia* belongs, the sepals and petals are both five in number and free (Fig. 632).

The lower overlapping petals are somewhat larger than the upper ones. Of the ten stamens the three upper ones are short and sterile while the other seven, the filaments of which are curved and convex below, diminish in length from above downwards. The anthers open by means of terminal pores. The pod is compressed and broad and flat. The flowers are borne in racemes in the axils of the leaves of the shrub, which is about a metre high. The bright green, equally pinnate leaves have small stipules at the base (Fig. 632). *Tamarindus indica* (Fig. 633) is a handsome tree, native to tropical Africa, but now planted throughout the tropics. Its broadly spreading crown of light foliage makes it a favourite shade-tree. The racemes of flowers are terminal on lateral twigs bearing equally pinnate leaves. The individual flowers are markedly zygomorphic (Fig. 631 *B*). The bract and two bracteoles are soon shed. The four sepals have a somewhat

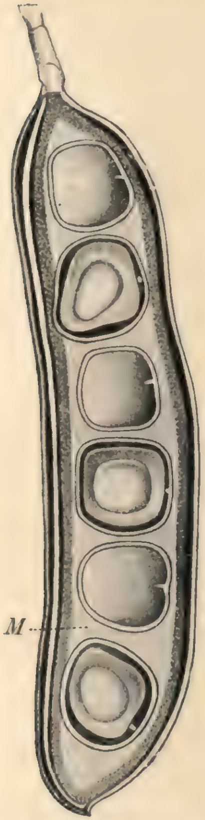


FIG. 634.—*Tamarindus indica.* Fruit in longitudinal section. *M*, the fleshy mesocarp. (After BERG and SCHMIDT.) *OFFICIAL.*

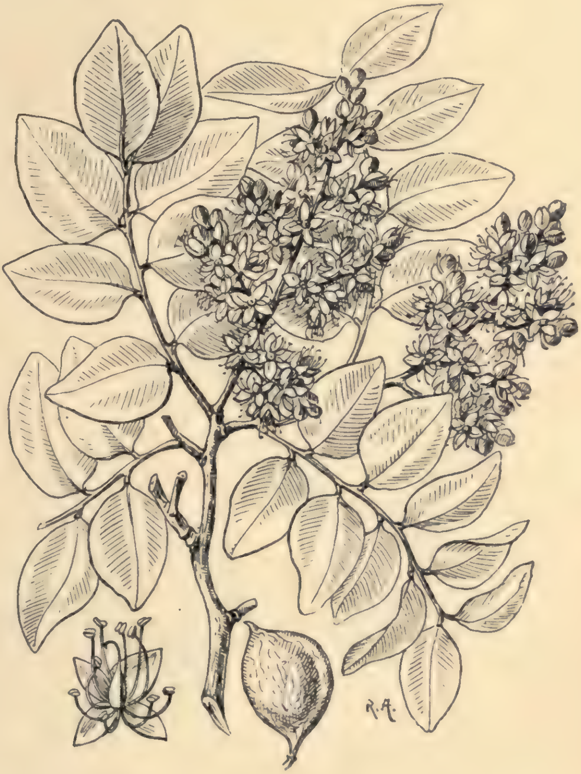


FIG. 635.—*Copaïfera Langsdorffii.* (½ nat. size) with a single flower (nat. size) and the fruit (reduced).

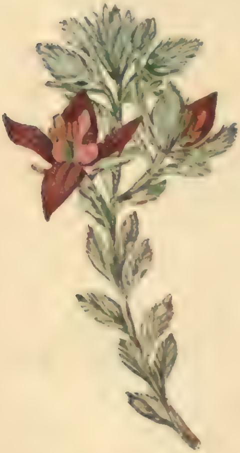


FIG. 636.—*Krameria triandra.* (⅓ nat. size. After A. MEYER and SCHUMANN.) *OFFICIAL.*

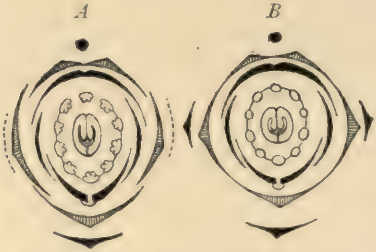


FIG. 637.—Floral diagrams of Papilionaceae. *A*, *Vicia Faba*; *B*, *Cytisus Laburnum.* (After EICHLER.)

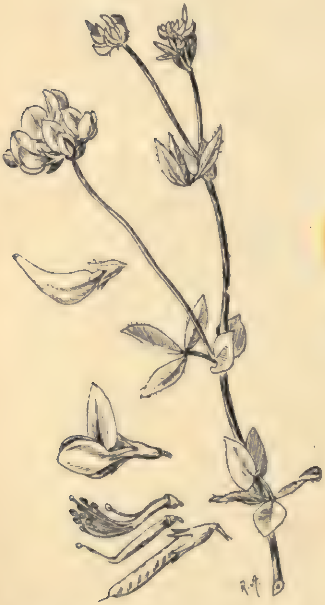


FIG. 638.—*Lotus corniculatus* (½ nat. size). Flowering shoot; flower, keel, stamens. Carpel (nat. size) and fruit (½ nat. size).

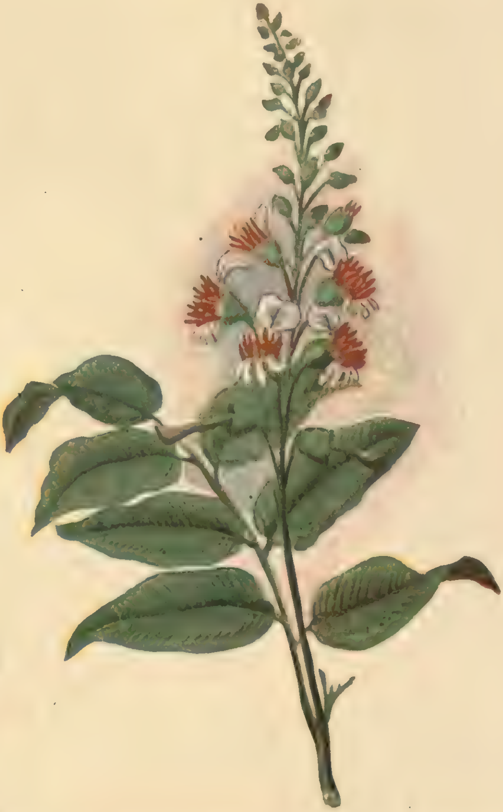


FIG. 639.—*Myroxylon Pereirae.* (⅔ nat. size. After BERG and SCHMIDT.) *OFFICIAL.*

cruciform arrangement. The three, red-veined, yellowish-white petals stand erect. The three stamens are coherent at the base and lie close to the easily movable curved carpel, so that the anthers and stigma project together. The fruit is peculiar. The pericarp is differentiated into an outer brittle exocarp, a succulent mesocarp, and a firm endocarp consisting of stone-cells investing the more or less numerous seeds individually (Fig. 634). *Humboldtia laurifolia* has hollow internodes inhabited by ants (Fig. 206, p. 236). The almost imperceptibly dorsiventral flowers of *Copaïfera* (Fig. 635) have no corolla ; the four sepals are succeeded by 8-10 free stamens. The fruit is one-seeded but opens when ripe. The seed is invested on one side by a succulent, irregularly limited arillus. None of the Caesalpiniaceae are British. *Cercis siliquastrum* from the Mediterranean region, which bears its flowers on the old woody stems (cauliflorous) (Fig. 631 A), and *Gleditschia triacanthos* (N. Am.) are sometimes cultivated as ornamental plants in gardens.

OFFICIAL.—SENNA INDICA, the pinnæ of *Cassia angustifolia* (Trop. East Africa and Arabia, cultivated at Tinnevelly in Southern India) ; SENNA ALEXANDRINA from *C. acutifolia* ; *Cassia fistula* (Trop. Am.) yields CASSIAE PULPA ; COPAIBA is obtained from *Copaïfera Langsdorfii* and other species ; TAMARINDUS from the succulent mesocarp of *Tamarindus indica* ; HAEMATOXYLI LIGNUM, the heart-wood of *Haematoxylon campechianum* (Trop. Am.) ; KRAMERIAE RADIX from *Krameria triandra*, a shrub growing in the Cordilleras. Flowers atypical ; the sepals brightly coloured within ; the corolla small. Three stamens opening by pores at the summit. Fruit spherical, prickly. Leaves simple, silvery white (Fig. 636).

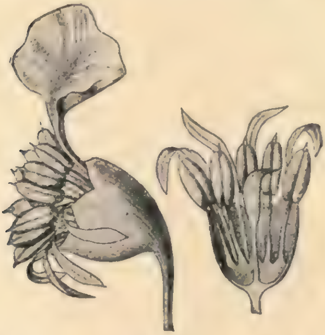


FIG. 640.—*Myroxylon Pereirae.* See Text. (Enlarged. After BERG and SCHMIDT.) *OFFICIAL.*

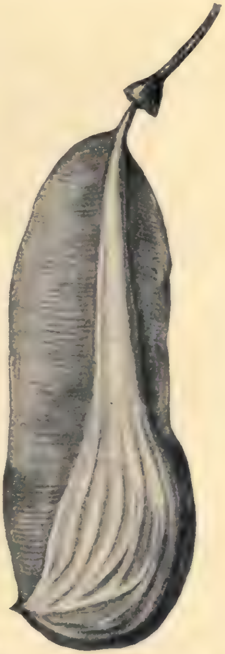


FIG. 641.—Fruit of *Myroxylon Pereirae* ($\frac{2}{3}$ nat. size). *OFFICIAL.*

Family 3. **Papilionaceae.**—Herbs, shrubs, or trees with, as a rule, imparipinnate leaves. Flowers always markedly zygomorphic. Calyx of five sepals. Corolla of five petals, papilionaceous, with descending imbricate æstivation (Fig. 637). Stamens 10 ; filaments

either all coherent into a tube surrounding the pistil or the posterior stamen is free. Seeds with a curved embryo.

The component parts of a papilionaceous flower are seen separately in Fig. 638. The posterior petal, which overlaps the others in the bud, is termed the standard (vexillum). The two adjoining, lateral petals are the wings (alæ), and the two lowest petals, usually coherent by their lower margins, together form the keel (carina). The upper ends of the stamens are usually free and curve upwards, as does also the style bearing the stigma.

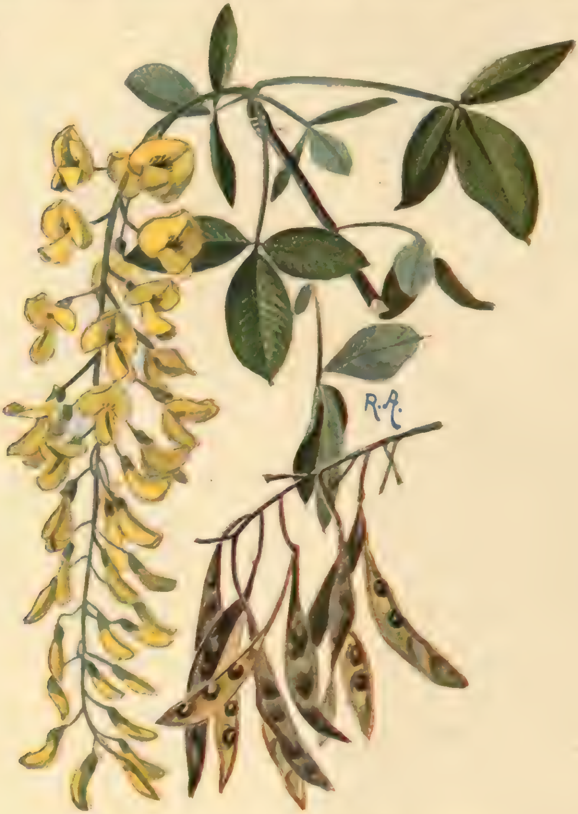


FIG. 642.—*Cytisus Laburnum* (½ nat. size). *POISONOUS.*

IMPORTANT SUB-FAMILIES AND GENERA.—The (1) *Sophoreae* and (2) *Podalyrieae* approach the Caesalpinaceae in having the stamens more or less free. The former is characterised by pinnate leaves, the latter by simple or palmate leaves. The genus *Myroxylon*, belonging to the Sophoreae, is of importance on account of the balsam obtained from species belonging to it. *Myroxylon Pereirae* is a tree of moderate height with alternate, imparipinnate leaves (Fig. 639). The flowers are borne in terminal racemes and have a large vexillum, the other petals remaining narrow and inconspicuous. The stamens are only coherent at the base, and bear conspicuous, reddish-yellow anthers (Fig. 640). The fruit is very peculiar. The ovary has a long stalk and bears two ovules near the tip. One of these develops into the seed of the indehiscent, compressed pod, which has a broad wing along the ventral suture and a narrower wing along the dorsal suture (Fig. 641). The bell-shaped calyx persists on the stalk. — 3. *Genisteae.* All ten stamens are coherent (Fig. 637 *B*). Leaves pinnate or simple, margin entire. *Genista*, *Sarothamnus*, *Lupinus*, *Cytisus* (Fig. 642). The Laburnum (*Cytisus Laburnum*) is one of the commonest ornamental trees of our gardens and grows wild in the Alps. It has tripinnate leaves and long pendulous racemes of yellow flowers. *C. Adami*, which is found occasionally in gardens, was supposed to have arisen by the grafting of *C. purpureus* on *C. Laburnum.* The racemes and flowers of one and the same individual sometimes resemble the former and sometimes the latter ancestral form (Fig. 247). The intermediate form is however sterile, and probably corresponds to an ordinary hybrid grafted on *C. Laburnum.* *Ulex*, Furze, a characteristic British plant. *Spartium*, distributed in the Mediterranean region. — 4. *Trifolieae.* Leaves trifoliate, serrate. Flowers aggregated in heads or in spikes or umbels. Stamens (9) + 1. Indehiscent fruits. *Trifolium*, Clover, with persistent calyx and corolla. *Medicago*, Medick, with deciduous corolla; fruit sickle-shaped or spirally twisted. *Melilotus*, Melilot, with racemose inflorescences. *Trigonella.* *Ononis*, Rest-Harrow. The increase in the amount of nitrogen in the soil effected by the root-tubercles (cf. p. 232, Fig. 204) of Leguminosae finds its practical application in European agriculture in the cultivation of species of *Trifolium*, *Medicago*, and *Lupinus.*—5. *Loteae.* Lotus, Bird's-foot Trefoil (Fig. 638). Leaves imparipinnate, lowest pair of leaflets owing to the absence of the petiole resembling stipules. *Anthyllis*, Kidney-Vetch. *Tetragonolobus.* — 6. *Galegeae* or *Astragaleae.* Leaves impari-

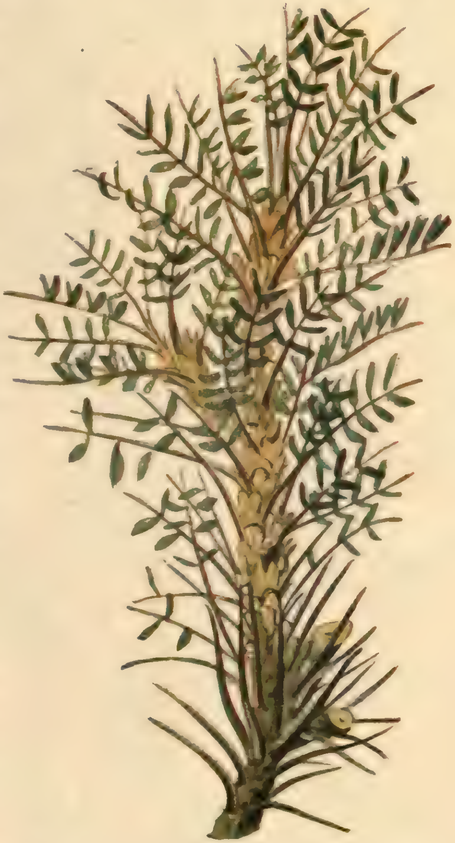


FIG. 643.—*Astragalus gummifer.* (½ nat. size. After A. MEYER and SCHUMANN.) *OFFICIAL.*

pinnate; a very large sub-family, the plants belonging to which show much diversity in habit. In species of *Astragalus*, which are low shrubs of the eastern Mediterranean region and of western Asia, the rhachis of the leaf persists as a sharply pointed thorn for years after the leaflets have fallen. These spines serve to protect the young shoots, leaves, and flowers (Fig. 643). Our native species are herbaceous. *Robinia* is an American tree of rapid growth with very brittle wood,

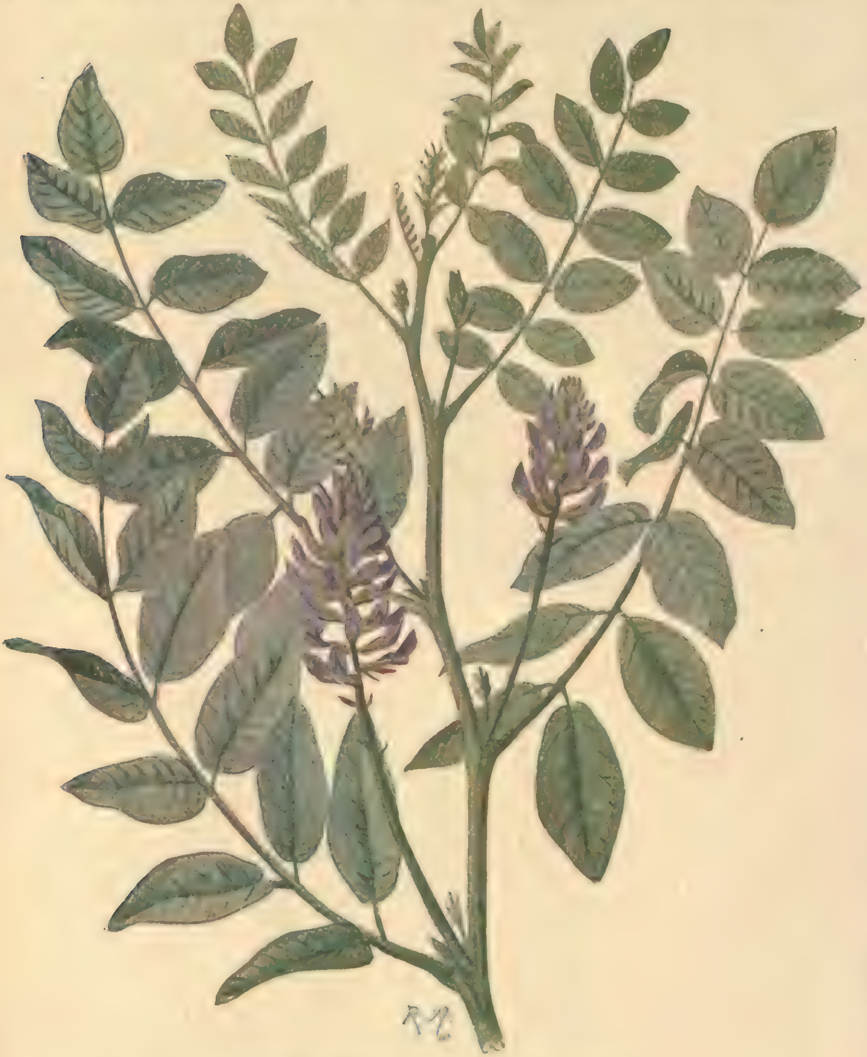


Fig. 644.—*Glycyrrhiza glabra* (½ nat. size). OFFICIAL.

which is often planted and known as False Acacia. *Glycyrrhiza*, Liquorice, is a native of S. Europe (Fig. 644). *Colutea, Caragana, Indigofera. Wistaria sinensis* is a climber with beautiful blue flowers, often grown against the walls of houses. —7. *Hedysareae*. Distinguished by the jointed pods, in which the seeds are isolated by transverse septa. *Coronilla* (Fig. 645). *Ornithopus sativus*, Bird's-Foot. *Arachis hypogaea*, Ground-nut, an important, oil-yielding fruit of the tropics and sub-tropics. After flowering the flower-stalks penetrate the soil in which the fruits ripen.—8. *Vicieae*. Leaves with terminal tendrils, corresponding to the terminal leaflet; the leaves may thus appear to be paripinnate. The cotyledons remain within the seed-coat and do not become green. Stamens (9) + 1. *Vicia*, Vetch; *Pisum*, Pea; *Ervum*, Lentil; *Lathyrus*, Everlasting Pea. *Faba*, the Broad-Bean, is an erect plant, without tendrils; the terminal leaflet is reduced to a bristle-shaped stump. 9. *Phaseoleae*. Twining plants with tripinnate leaves. Cotyledons usually come above ground and turn green. Stamens (9) + 1. *Phaseolus*, Kidney Bean. *Physostigma*.

POISONOUS. — Among our common Leguminosae only *Cytisus Laburnum* is extremely poisonous. The other species of the genus, *e.g. C. alpinus, C. purpureus, C. Weldeni*, and *C. biflorus* are poisonous, but are more rarely met with than the ordinary Laburnum. *Coronilla varia* (Fig. 645), with umbels of rose-coloured flowers, and *Wistaria sinensis* are also poisonous.

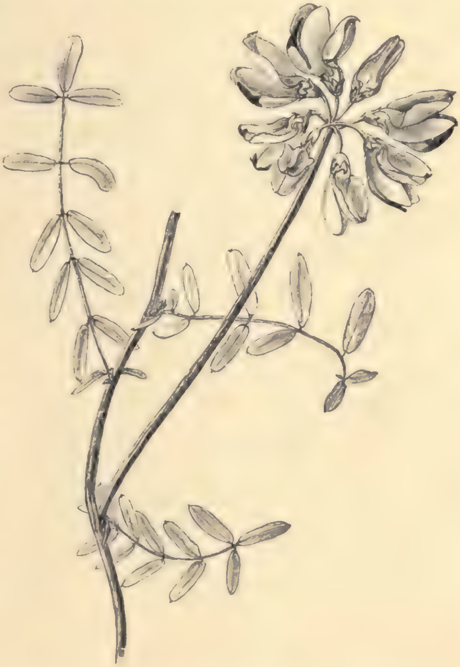


FIG. 645.—*Coronilla varia* (nat. size). *POISONOUS.*

OFFICIAL. — *Astragalus gummifer* and other species yield TRAGACANTHA. GLYCYRRHIZAE RADIX is obtained from *Glycyrrhiza glabra*. *Spartium scoparium* yields SCOPARII CACUMINA. *Physostigma venosum*, a West African climber, yields PHYSOSTIGMATIS SEMINA, Calabar Bean. *Andira araroba*, a Brazilian tree, contains a powdery excretion in cavities of the stem called ARAROBA; CHRYSAROBINUM is obtained from this. The heart-wood of *Pterocarpus santalinus*, an East Indian tree, is PTEROCARPI LIGNUM. KINO is obtained from the juice flowing from incisions in the trunk of *Pterocarpus marsupium*. *Myroxylon toluifera* (S. America) yields BALSAMUM TOLUTANUM, and *M. Pereirae* (San Salvador) BALSAMUM PERUVIANUM.

Order 13. Gruinales

The flowers of the majority of the plants belonging to this order are hermaphrodite, pentamerous, and radially symmetrical, with a superior, septate ovary. K 5, C 5, A 5 + 5, G $(\overline{5})$. When the flowers are zygomorphic they frequently exhibit reduction. Stamens coherent at the base, obdiplostemonous or haplostemonous. Nectaries to the outer side of the stamens or as a circular disc within the stamens. Ovules, usually pendulous; micropyle directed upwards.

The **Terebinthinae** are included in this order as above defined. Their distinguishing characteristic is the intrastaminal, annular nectary.

Family 1. **Geraniaceae.** — Herbs or small shrubs with, as a rule, alternate, stalked, palmately veined leaves. Flowers conspicuous, solitary in the leaf axils or forming cymose or umbellate inflorescences. They are usually actinomorphic; in *Pelargonium* zygomorphic and provided with a spur. Stamens 10 or 5. Two ovules in each loculus. When ripe the five beaked carpels separate from a central column, and either open to liberate the seeds, or remain closed and by the hygroscopic movements of the awn-like portion bury the seed in the soil (Figs. 646, 647. Cf. Fig. 222, p. 271).

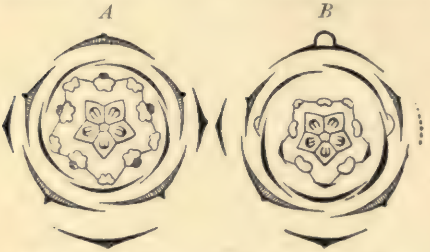


FIG. 646.—Floral diagrams of Geraniaceae. *A*, *Geranium pratense*; *B*, *Pelargonium zonale*. (After EICHLER.)

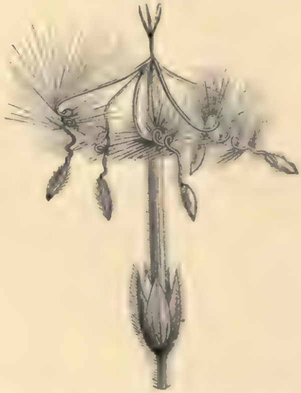


FIG. 647.—Fruit of *Pelargonium inquinans*, × 3. (After BAILLON.)

Geranium with ten stamens and *Erodium* with five stamens occur in Britain. Numerous species of *Pelargonium* from the Cape are cultivated as ornamental plants; the peculiar scent of the vegetative organs is due to the ethereal oil secreted by the glandular hairs.

Family 2. **Tropaeolaceae.**—*Tropaeolum majus*, Indian Cress, climbs by help of the petioles. Flowers zygomorphic, spurred, with 8 stamens and 3 carpels. Fruit, a capsule. Leaves peltate (cf. Fig. 191).

Family 3. **Oxalidaceae.** — Leaves compound, in some species irritable to mechanical stimuli (*Biophytum. Oxalis acetosella*, Wood Sorrel, cf. p. 295).

Family 4. **Linaceae.**—Herbs or shrubs with alternate, narrow, entire leaves. Flowers actinomorphic. Stamens coherent at the base; those opposite the petals developed as staminodes. Ovary 5-locular, each loculus incompletely divided by a false septum; in each chamber is one pendulous ovule. Fruit a capsule (Fig. 648 A-C). *Linum usitatissimum*, Flax, has long been in cultivation. It is an annual, and bears numerous blue flowers, which last only a short time, in racemose cincinni. The flower has five, free styles. The stem bears numerous small, narrow leaves. The bast-fibres after proper preparation are woven into linen. The seeds yield oil.

OFFICIAL.—LINUM, the seeds of *Linum usitatissimum.*

Family 5. **Balsaminaceae.**—Succulent herbs, with translucent stems, sometimes swollen at the nodes, and simple leaves. Flowers zygomorphic with five free stamens. Capsule dehiscing elastically. *Impatiens noli tangere, I. parviflora*, and *I. Balsamina.* Regarding the occurrence of cleistogamous flowers in Impatiens cf. p. 518.

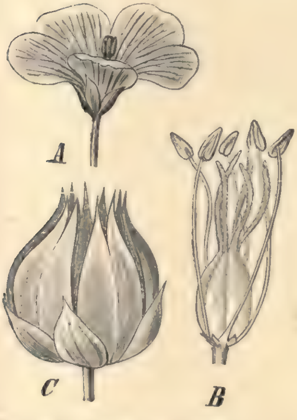


FIG. 648.—*Linum usitatissimum. A*, Flower; *B*, androecium and gynaeceum; *C*, capsule after dehiscence. (*A*, nat. size; *B*, *C*, × 3). *OFFICIAL.*

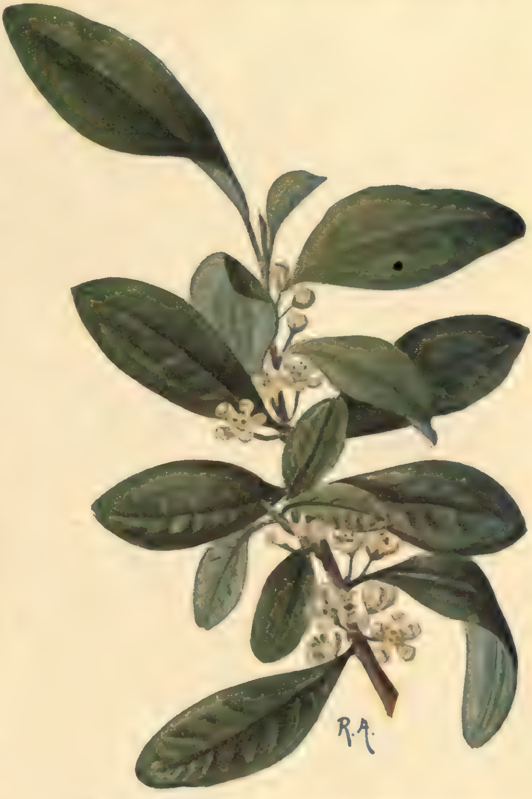


FIG. 649.—*Erythroxylon Coca.* ($\frac{2}{3}$ nat. size.) *OFFICIAL.*

Family 6. **Erythroxylaceae.**—*Erythroxylon Coca* is a small Peruvian shrub, with entire, simple leaves and axillary groups of small, white flowers. Petals with appendages. Stamens 10, united at the base into a tube, G (3), but only one loculus of the ovary is fertile. Fruit, a one-seeded drupe (Fig. 649).

OFFICIAL.—From *E. coca* COCAE FOLIA, which yield COCAINA, are obtained.

Family 7. **Zygophyllaceae.**—Floral formula typically $K5,\ C5,\ A5+5\ \underline{G(5)}$; with an intrastaminal disc.

OFFICIAL.—*Guiacum officinale*, a West Indian tree with opposite, paripinnate leaves. Ovary bicarpellary, bilocular. Fruit winged. It yields GUIACI LIGNUM and GUIACI RESINA.

Family 8. **Rutaceae.**—For the most part shrubs or trees, rarely herbs, with alternate, pinnate leaves. Flowers usually actinomorphic, tetramerous or pentamerous with a large intrastaminal disc. Oil-containing cavities in all the members.

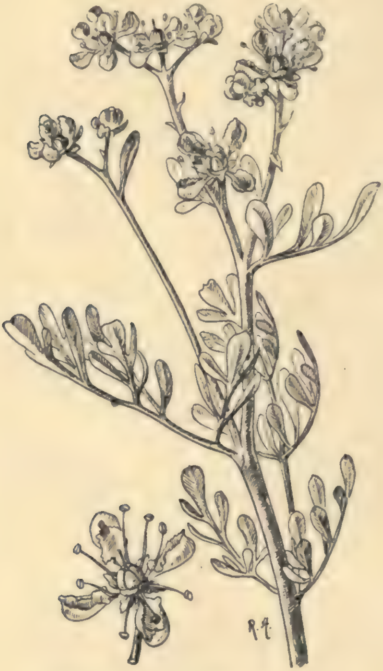


FIG. 650.—*Ruta graveolens* (½ nat. size).

IMPORTANT GENERA. — *Ruta graveolens* (Fig. 650), the Rue, is a somewhat shrubby plant with pinnately divided leaves. The terminal flowers of the dichasial inflorescences are pentamerous in robust examples; all the other flowers are tetramerous. *Dictamnus Fraxinella* has panicles of conspicuous, dorsiventral flowers; the carpels are free in their upper portions. The important genus *Citrus* (29) has peculiarly constructed flowers (Figs. 651, 652). The numerous stamens are united in bundles and arranged in a single whorl. The number of carpels is also increased. The fruit is a berry; the succulent portion is formed of large cells with abundant cell-sap which project into and fill up the loculi of the ovary. The leaves of many species are simple and provided with more or less winged petioles. Other species have trifoliate leaves and the articulation at the base of the lamina shows that the apparently simple leaves correspond to imparipinnate leaves, of which only the terminal leaflet is developed. The thorns at the base of the leaf are derived by modification of the first leaves

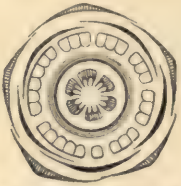


FIG. 651.—Floral diagram of *Citrus vulgaris*. (After EICHLER.)

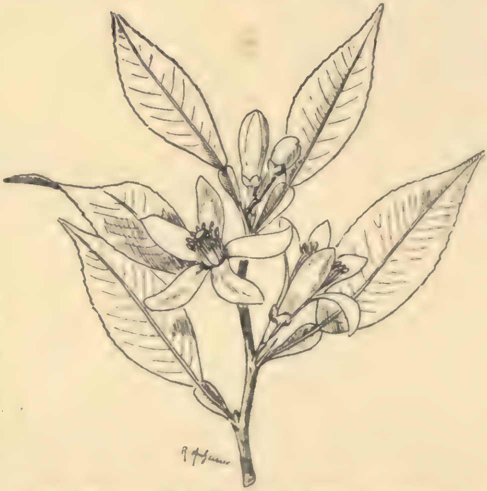


FIG. 652.—*Citrus vulgaris* (½ nat. size). *OFFICIAL.*

of the axillary bud. *Citrus* is originally an East Asiatic genus; a number of species inhabit the warmer valleys of the Himalayas. All the important cultivated forms have been obtained from the Chinese. *Citrus decumana*, the Shaddock, is tropical; *C. medica* is the form which was known to the Greeks in the expeditions of Alexander as the Median apple. It is now widely spread and has a number of varieties of which *Citrus* (*medica*) *Limonum* is the Lemon. This tree was introduced into the Mediterranean region in the third or fourth century. *Citrus* (*medica*) *Bajoura* has thick-skinned fruits from which citron is obtained. *Citrus Aurantium* occurs in two distinct forms, *C.* (*Aurantium*) *vulgaris* and *C.* (*Aurantium*) *sinense*. The latter is a variety of the Bitter Orange tree of apparently Chinese origin, and already comes more or less true to seed. The name Orange, which is introduced into many languages and is derived from the Sanscrit word Nagarunga, points to the ancient cultivation of

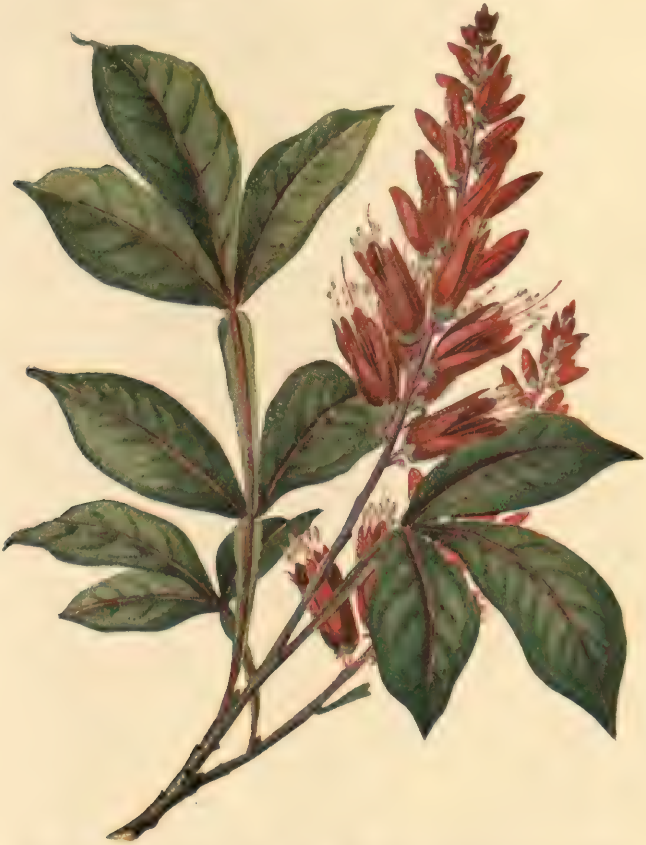


FIG. 653.—*Quassia amara*. (Nat. size. After BERG and SCHMIDT.) *OFFICIAL*.

the plant in India. The name was first applied to the Bitter-fruited Orange, which found its way west much earlier that the sweet variety, and was subsequently applied to the latter. *Citrus nobilis*, the Mandarin, is also of Chinese origin.

OFFICIAL.—*Citrus Aurantium*, var. *Bigaradia*, yields AURANTII CORTEX SICCATUS, AURANTII CORTEX RECENS, and AQUA AURANTII FLORIS. *Citrus medica*, var. *limonum*, gives LIMONIS CORTEX, and LIMONIS SUCCUS. BUCHU FOLIA are obtained from *Barosma betulina*. CUSPARIAE CORTEX from *Cusparia febrifuga*. JABORANDI FOLIA from *Pilocarpus jaborandi*, a tree-like shrub with large, imparipinnate leaves, native of Eastern Brazil.

Family 9. **Simarubaceae.**—K 5, C 5, A 5+5, G 5. Carpels free. No oil glands. Contain bitter principles.

OFFICIAL.—QUASSIAE LIGNUM from *Picrasma excelsa* (West Indies) and *Quassia amara* (Surinam). The latter (Fig. 653) is a small tree with beautiful leaves and showy flowers.

Family 10. **Burseraceae.**—Woody plants with resin passages. Fruit, a drupe. *Commiphora abyssinica* and *C. Schimperi* are trees found in Arabian East Africa. *Boswellia Carteri* and *B. Bhau Dajianae* are small trees (30) from the same region which yield OLIBANUM. *Canarium*.

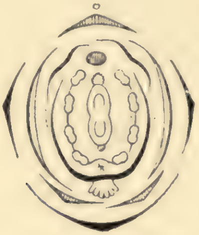


FIG. 654.—Floral diagram of *Polygala myrtifolia*. (After EICHLER.)

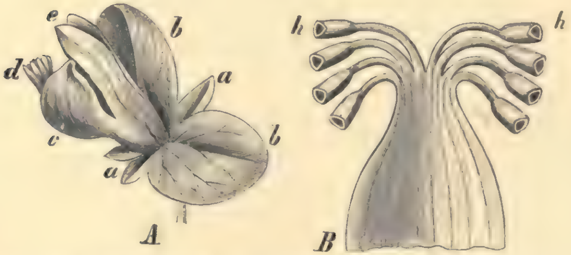


FIG. 655.—*Polygala Senega*. *A*, Flower; *a*, small; *b*, large sepals; *c*, keel; *e*, lateral sepals; *d*, androecium. *B*, androecium; *h*, anthers (magnified). (After BERG and SCHMIDT.) *OFFICIAL*.

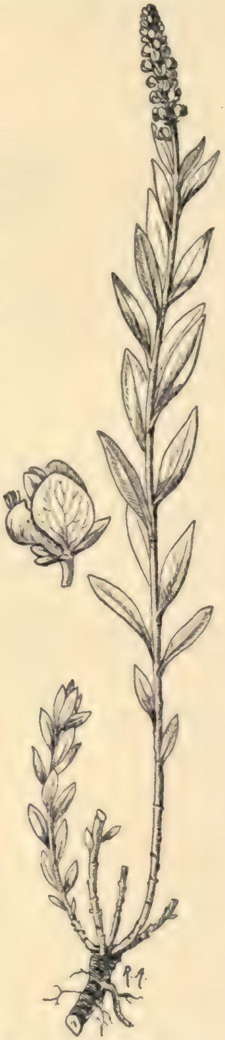


FIG. 656.—*Polygala Senega*. (½ nat. size). *OFFICIAL*.

OFFICIAL.—MYRRHA, Myrrh, from *Balsamodendron Myrrha* and other species.

Family 11. **Polygalaceae.**—Herbs or shrubs with small simple leaves and dorsiventral flowers. K5, C3, A(8), G(2). The two lateral sepals are petaloid. Three petals, the lowest of which forms a keel. Stamens 8, coherent into a tube. Anthers opening by pores. Ovary bilocular, formed of two carpels; a single ovule in each loculus (Figs. 654-656). *Polygala chamaebuxus* is a small shrubby plant occurring in the Alps. *P. vulgaris* and *P. amara* occur in Britain.

OFFICIAL.—*Polygala Senega* (North America) yields SENEGAE RADIX.

Order 14. Tricoccae (31)

The large Family of the **Euphorbiaceae** which belongs to this order is of much greater importance than the small family which is here placed along with it. The plants belonging to the Euphorbiaceae are of very diverse habit. The order includes herbs, shrubs, leafless succulent plants, trees with normal foliage, and others with scale leaves and assimilating phylloclades. The plants agree, however, in possessing unisexual, actinomorphic flowers, with a simple perianth or with no trace of the latter. Androecium diplostemonous or stamens numerous. The female flowers are especially characterised by the superior, trilocular ovary formed of three carpels; in each loculus are one or two pendulous ovules with a ventral raphe, and the micropyle directed upwards and outwards.

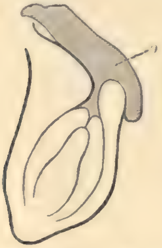


FIG. 657.—Ovule of *Euphorbia dioica* showing the obturator. (After PAX in *Engler-Prantl.*)

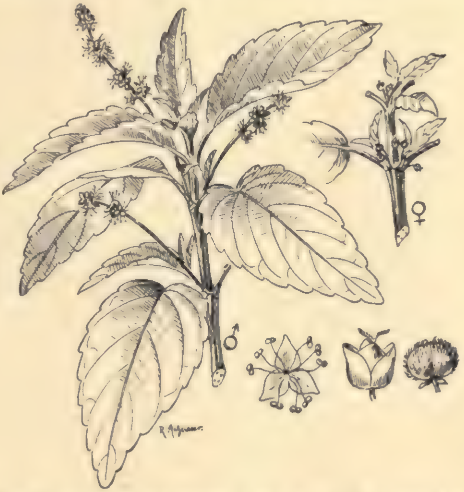


FIG. 658.—*Mercurialis annua* (½ nat. size). Male plant in flower and single male flower. Portion of a female plant, single female flower and fruit. *POISONOUS.*

The micropyle is covered by a placental outgrowth called the obturator (Fig. 657); this assists in conducting and nourishing the pollen-tube, and disappears after fertilisation. The CARUNCULA, which is formed from the outer integument (Fig. 662 *D*), persists on the other hand in the seed; the separation of the latter from the placenta is assisted by it.

The fruit is a capsule, the outer walls of which contract elastically away from a central column, and thus open the loculi.

IMPORTANT GENERA.—Many Euphorbiaceae are diœcious or monœcious, and have flowers of relatively simple construction. Thus *Mercurialis* (Fig. 658), two species of which occur in Britain, is characterised by its bicarpellary ovary. *Croton* is a tropical genus including valuable official plants, *C. Eleuteria* and *C. Tiglium*. In the Spurges (*Euphorbia*), of which there are several British species, a number of the extremely simply constructed flowers are grouped in a complicated inflorescence termed a CYATHIUM (Figs. 659-662). This consists of a naked, terminal, female flower, borne on a long bent stalk surrounded by a number of groups of male flowers. Each of the latter is stalked and consists of a single stamen, the limit between which and the flower-stalk is distinguishable. In some cases the female flower and each male flower are provided with a small perianth. The whole cyathium, which is an inflorescence, is always enclosed by five involucral bracts ; alternating with these are four nectar-secreting glands, the presence of which increases the likeness between the cyathium and a flower. The fifth gland is wanting, and the

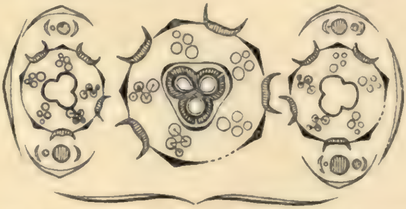


FIG. 660.—Diagram of a dichasial branch of *Euphorbia*, with three cyathia, only the middle one of which has a fertile female flower. (After EICHLER.)

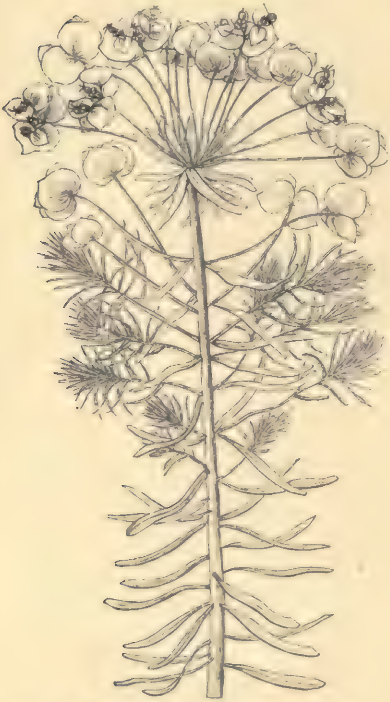


FIG. 659.—*Euphorbia cyparissias* (⅔ nat. size). *POISONOUS.*

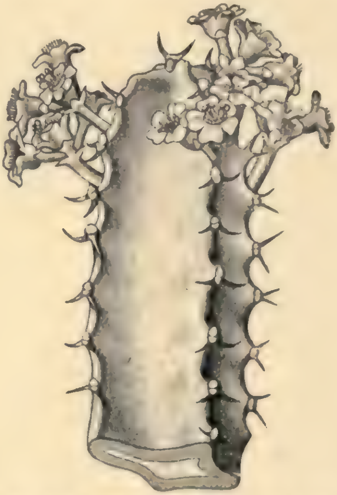


FIG. 661.—*Euphorbia resinifera.* (Nat. size. After BERG and SCHMIDT.)

inverted female flower hangs down in the gap left. Between the groups of male flowers, which stand opposite to the bracts (Fig. 660), are branched hairs which are visible when the cyathium is cut through longitudinally (Fig. 662 *B*). The cyathia are usually grouped in dichasia, and these in turn form an umbellate inflorescence, with three to many branches. It often happens that the female flower is only developed in some of the cyathia, remaining rudimentary in the others. Many species of *Euphorbia*, especially the African species, are succulent-stemmed plants resembling *Cacti* in general appearance (cf. Fig. 661).

Euphorbia, like many but not all the other plants of the family, contains a milky juice, which is secreted in non-septate latex-tubes. This juice, which in many cases is poisonous, exudes wherever the plant is wounded.

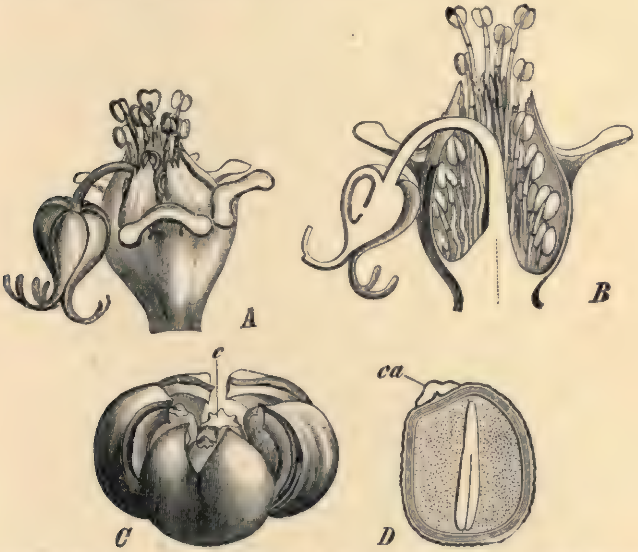


FIG. 662.—*Euphorbia Lathyris.* *A*, Cyathium (× 5). *B*, Cyathium cut through longitudinally (× 7). *C*, Fruit after dehiscence showing the central column (*c*). *D*, Seed in longitudinal section showing the embryo embedded in the endosperm; *ca*, caruncula (× 4). (*A-D* after BAILLON.)

An important constituent of the latex of species of *Hevea* (*H. Sieberi*, *discolor*, *rigidifolia*, *paucifolia*, *lutea*, *guyanensis*, *Spruceana*) is CAOUTCHOUC. As Para Rubber obtained in the tropics of South America, especially in the Amazon region, this affords about one half of the total rubber supply. In addition *Manihot Glaziovii*, another South American plant of this order, which yields Ceara Rubber, must be mentioned. A nearly related plant, *Manihot utilissima*, provides in its tuberous roots a very important food in the tropics. The starch obtained from these roots forms mandioc or cassava meal, the finest varieties of which, as tapioca or Brazilian arrowroot, are of commercial importance. The shrub, which is a native of Brazil, is now cultivated throughout the tropics.

Ricinus communis (Fig. 663) is a tall shrub of tropical Africa. In our climate it is annually killed by the frost. The hollow stem bears large palmately divided leaves. The terminal inflorescences (Fig. 664) are overtopped by vegetative lateral branches. The male flowers, situated towards the base, have a membranous calyx of 4-5 sepals, enclosing the branched stamens; the end of each branch bears a theca. The female flowers, nearer the summit of the inflorescence, have 3-5 sepals and a large tripartite ovary. The latter is covered with warty prickles, and bears three large, bifid, red stigmas. In each loculus of the fruit is a mottled seed with a whitish caruncula. *Mallotus philippinensis.*

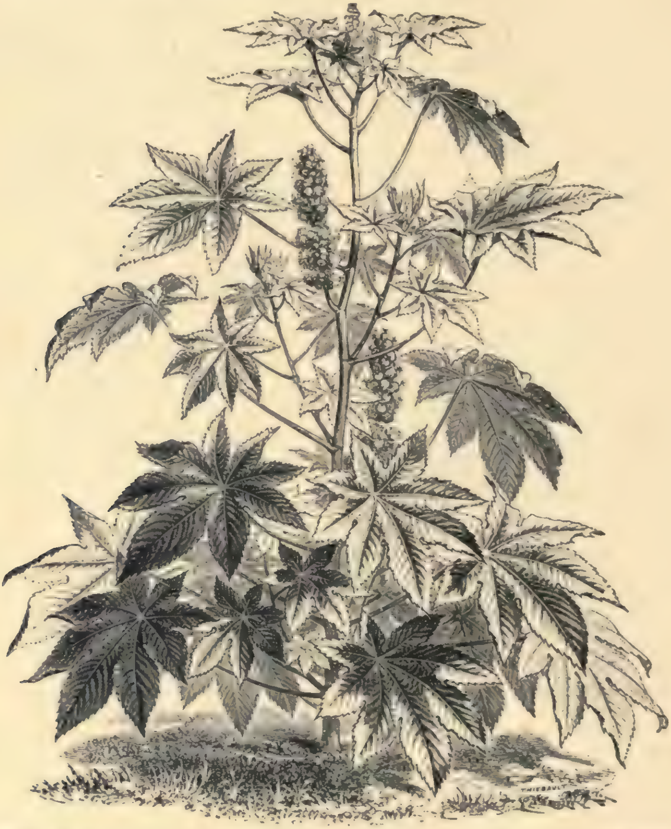


FIG. 663.—*Ricinus communis*, greatly reduced. (After BAILLON.) *POISONOUS* and *OFFICIAL.*

OFFICIAL.—*Croton Eleuteria* (Bahamas) yields CASCARILLA. *C. tiglium* (East Indies), OLEUM CROTONIS. OLEUM RICINI, Castor Oil, is obtained from *Ricinus communis.*

The **Callitrichaceae** are a small family of water plants, with naked, unisexual flowers. Stamen 1, carpel 1.

Order 15. Sapindinae

This order includes trees and shrubs of very different appearance, with cyclic flowers. The latter exhibit reduction in the perianth, androecium, and gynaeceum.

One or two ovules are contained in each chamber of the ovary; when the ovules are erect the raphe is ventral, when they are pendulous it is dorsal; this differs from what is the case in the Euphorbiaceae.

Family 1. **Buxaceae.** — *Buxus sempervirens*, the Box, is a poisonous, evergreen shrub with very close wood, native of Central and Western Europe. In the axils of small, decussate bracts stand capitate inflorescences, consisting of a terminal, trimerous, female flower, and a number of tetramerous male flowers.

Family 2. **Anacardiaceae.** — Distributed in the tropics and warm temperate regions. Ovary of 1-3 carpels. Fruit usually a one-seeded drupe. Schizogenous resin passages. *Mangifera indica*, an important fruit tree of the tropics. Species of *Rhus* yield Japan lacquer. *R. toxicodendron*, a North American climbing shrub, is extremely poisonous. Species of *Pistacia* (Mediterranean region) have pinnate leaves. *P. vera* is cultivated on account of its drupaceous fruits called Pistachio nuts.

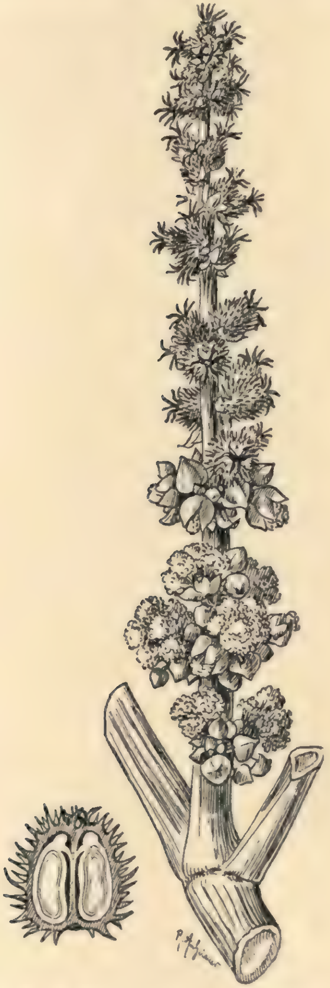


FIG. 664.—*Ricinus communis.* Inflorescence (½ nat. size); young fruit cut through longitudinally. *OFFICIAL.*

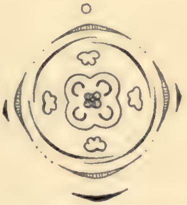


FIG. 665.—Floral diagram of *Ilex aquifolium.* (After EICHLER.)

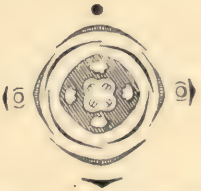


FIG. 666.—Floral diagram of *Euonymus europaea.* (After EICHLER.)

Family 3. **Aquifoliaceae.** — *Ilex aquifolium*, the Holly, is an evergreen shrub or tree of Western Europe (Fig. 665). K4, C4, A4, G(4). In each loculus of the ovary is a pendulous ovule. *I. paraguariensis* in extra-tropical South America yields Paraguay Tea or Matè.

Family 4. **Celastraceae.**—*Euonymus europaea*, the Spindle tree (Figs. 666, 667), is a British shrub with inconspicuous flowers; K 4, C 4, A 4, G(4). The stamens are inserted at the margin of a large disc; two ovules in each loculus. In autumn the bright red arillus of the seeds, which hang by their stalks from the opened pale red capsule, makes the fruit conspicuous.

Family 5. **Aceraceae.**—Trees with opposite leaves. The flowers show a tendency to become unisexual by abortion of stamens or carpels. Disc intra- or extra-staminal. Carpels two. Fruit, a winged schizocarp (Fig. 668). In Britain *Acer campestre* and *A. pseudoplatanus*. The characteristic lobed outline and palmate nervation of the leaves, as a rule, enable the genus to be readily recognised.

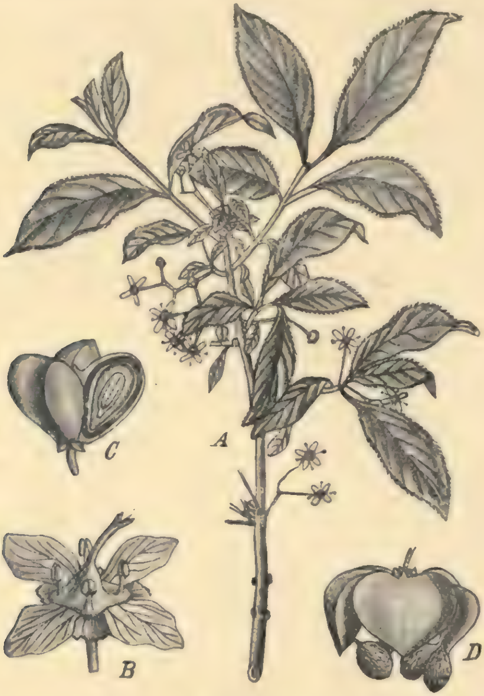


FIG. 667.—*Euonymus europaea*. *A*, Flowering branch (reduced); *B*, a flower (magnified); *C*, *D*, the fruit (nat. size). (*B-D*, after ENGLER-PRANTL.) *POISONOUS*.

Family 6. **Sapindaceae.**—Tropical trees or shrubs usually with obliquely zygomorphic flowers with an extra-staminal disc.

The crushed seeds of *Paullinia cupana*, a liane of tropical Brazil, yield GUARANA.

Family 7. **Hippocastanaceae.**—Closely related to the Sapindaceae. *Aesculus*, Horse-chestnut. *Aesc. Hippocastanum*, the White Horse-chestnut, is a tree of hilly regions of the eastern Mediterranean (Fig. 485 *B*). *Aesc. pavia*, the Red

Horse-chestnut, is a native of the mountains of the Atlantic side of North America. Both are commonly cultivated.

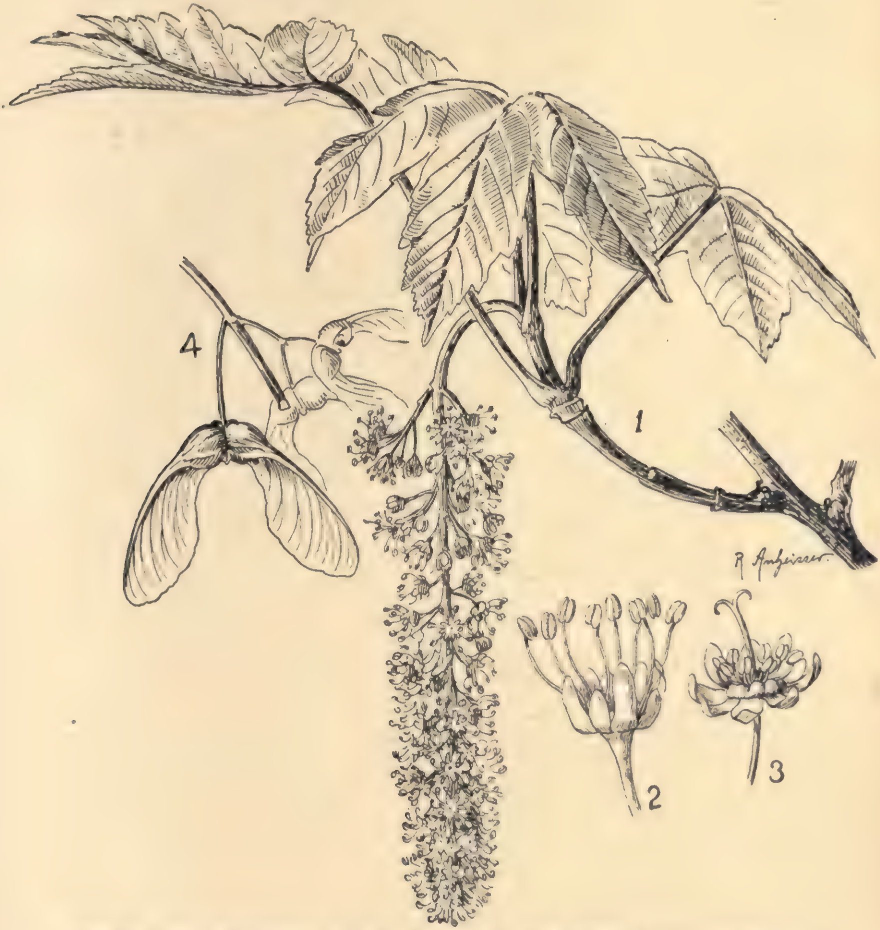


FIG. 668.—*Acer pseudoplatanus* ($\frac{1}{2}$ nat. size). *1*, Branch with pendulous terminal inflorescence. *2*, Male flower. *3*, Female flower. *4*, Fruit. (*2* and *3* enlarged.)

Order 16. Frangulinae

Shrubs or trees with inconspicuous, actinomorphic, tetramerous or pentamerous flowers. There is only one whorl of stamens, which are antipetalous. Flowers hypogynous or perigynous. Ovary composed of two to four carpels with one or two erect ovules in each loculus. Disc intrastaminal.

Family 1. **Rhamnaceae.**—The only native genus of this family, which is distributed in the tropics, is *Rhamnus*, the Buckthorn (Figs. 669-671).

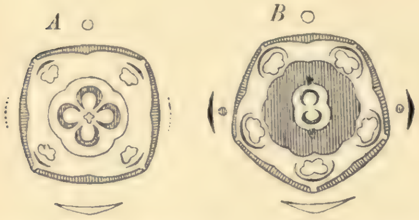


FIG. 669.—Floral diagrams of A, *Rhamnus cathartica* (represented as hermaphrodite) and *B*, *Rh. Frangula*. (After EICHLER.)

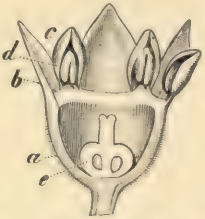


FIG. 670.—*Rhamnus Frangula*. Flower cut through longitudinally. *a*, Receptacle; *b*, calyx; *c*, petal; *d*, a stamen; *e*, pistil (magnified). (After BERG and SCHMIDT.)

Rh. Frangula, the Berry-bearing Alder, is a shrub with alternate, entire leaves provided with small stipules. The flowers are solitary or in groups in the axils of the leaves. K5, C5, A5, G(2). The floral receptacle forms a cup-shaped disc.

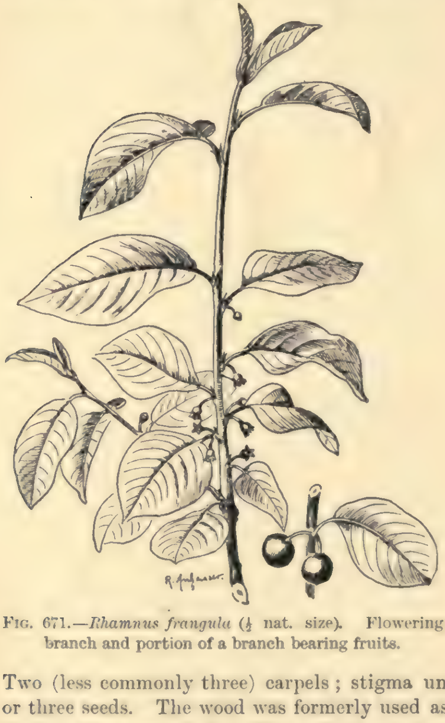


FIG. 671.—*Rhamnus frangula* (½ nat. size). Flowering branch and portion of a branch bearing fruits.

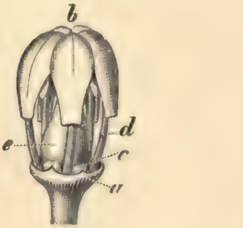


FIG. 672.—*Vitis vinifera*. Opening flower. *a*, Calyx; *b*, corolla; *c*, disc; *d*, stamens; *e*, ovary (magnified). (After BERG and SCHMIDT.)

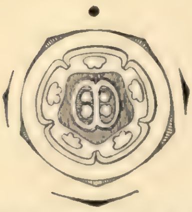


FIG. 673.—Floral diagram of *Ampelopsis hederacea*. (After EICHLER.)

Two (less commonly three) carpels; stigma undivided. Fruit, a drupe with two or three seeds. The wood was formerly used as a source of charcoal for the manufacture of gunpowder. *Rh. catharticus* has usually spiny branches bearing opposite leaves with serrate margins. Flowers tetramerous throughout, diœcious by suppression of stamens or carpels; female flower with four free styles and a four-seeded drupe. Seeds with a dorsal furrow. *Colletia spinosa* and *C. cruciata* are leafless South American shrubs; the thorns of the former are cylindrical, those of the latter flattened laterally.

OFFICIAL.—*Rhamnus purshianus* yields CASCARA SAGRADA or RHAMNI PURSHIANI CORTEX.

Family 2. **Vitaceae.**—Shrubby plants climbing by means of tendrils; leaves palmately lobed or divided. Flowers hypogynous. Ovary composed of 2-4 carpels and with a corresponding number of loculi. Two ovules in each loculus. Disc often consisting of separate glands (Figs. 672, 673).

IMPORTANT GENERA.—*Vitis*, climbing shrubs of the northern hemisphere. *Vitis vinifera*, the Grape Vine, is a cultivated plant with numerous races and varieties. The tendrils correspond to shoots and stand opposite to the leaves; they are at first terminal, but become displaced to one side by the development of the axillary shoot. The whole shoot is thus a sympodium. The original relation between the tendrils and the axillary shoots, which are both recognisable at the growing point, cannot be completely followed in the ontogeny. The inflorescence is a panicle taking the place of a tendril; intermediate forms between inflorescences and tendrils are of frequent occurrence. Calyx only represented by a small rim; Corolla thrown off when the flower opens. Currants are the seedless fruits of *Vitis vinifera*, var. *apyrena*. Species of *Ampelopsis* distributed in North America and Asia go by the name of Wild Vines; some of them have tendrils with adhesive disc (Fig. 29, p. 27). *Cissus* is a large, exclusively tropical genus.

OFFICIAL.—UVAE, Raisins from *Vitis vinifera*.

Order 17. Columniferae

The essential character of this order is afforded by the androecium of the regularly pentamerous, actinomorphic, hermaphrodite flowers. One of the two whorls of stamens, usually the outer one, is suppressed or only represented by staminodes, while the other whorl has undergone a greater or less increase in the number of its members by chorisis. The branching is frequently accompanied by cohesion of the filaments. The carpels also sometimes exhibit an increase in number as a result of branching. The superior ovary is then divided into a corresponding number of loculi.

Family 1. **Tiliaceae.**—For the most part trees or shrubs, less commonly herbs, with simple, stalked leaves provided with deciduous stipules. Calyx polysepalous. Æstivation of calyx and corolla valvate. Stamens completely free from one another with introrse anthers. A 5 + 5, or only the inner whorl is present and has usually undergone branching (Fig. 674). Ovary with two to many loculi, and one to many ovules in each loculus. Style simple.

Most of the genera are tropical. The herbaceous species of *Corchorus* yield Jute. In Britain two species of *Tilia*, Lime, occur. These are stately trees with two-ranked, petiolate leaves, the stipules of which are soon shed. The leaves, which have a serrate margin, are asymmetrical. The inflorescence (Fig. 675 *A*) is coherent with a bract for half its length; this serves as a wing in the distribution of the fruit. A second bract at the base protects the axillary bud, which will expand in the succeeding season. Below the terminal flower are three small bracteoles; the lowest of these is sterile while the two upper ones have single flowers in their axils. Each of these flowers has a pair of bracteoles which serve as the subtending leaves for further branching. The umbel-like inflorescence of the Lime is thus composed of dichasia; *Tilia platyphyllos* has 3-7, *T. parvifolia* 11 or more flowers in the inflorescence. The hairy ovary has two ovules in each of its five loculi. The fruit only contains one seed (Fig. 675 *B*).

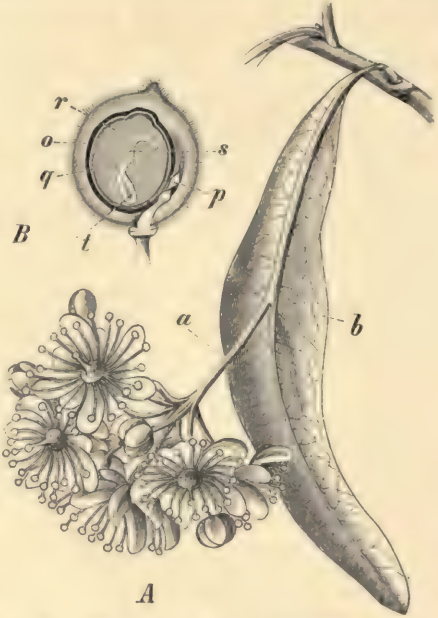


FIG. 675.—*Tilia ulmifolia.* *A*, Inflorescence (*a*), with bract *b* (nat. size). *B*, Longitudinal section of fruit (magnified); *o*, pericarp; *p*, atrophied dissepiment and ovule; *q*, seed; *r*, endosperm; *s*, embryo; *t*, its radicle. (After BERG and SCHMIDT.)

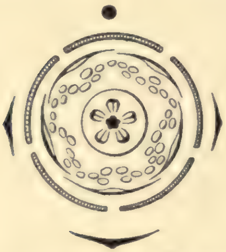


FIG. 674.—Tiliaceae. Floral diagram (*Tilia*). (After EICHLER.)

Family 2. **Sterculiaceae** (32).—Tropical herbs, shrubs, or trees, with simple leaves and deciduous stipules. Flowers with a gamosepalous calyx. Corolla twisted in the bud. Stamens coherent to form a tube; the antisepalous stamens are staminodial, the antipetalous stamens are often increased in number. Anthers extrorse.

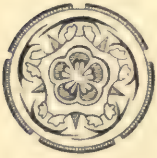


FIG. 676.—Sterculiaceae. Floral diagram (*Theobroma*). (After EICHLER.)

IMPORTANT GENERA.—The most important plant is the Cocoa tree (*Theobroma Cacao*, Figs. 676, 677). It is a native of tropical Central and South America, but has long been cultivated. The increasing demand has led to its being grown with more or less success in many tropical colonies. It is a low tree with short-stalked, firm, brittle, simple leaves of large size, oval shape, and dark green colour. The young leaves are of a bright red colour, and, as in many tropical trees, hang limply

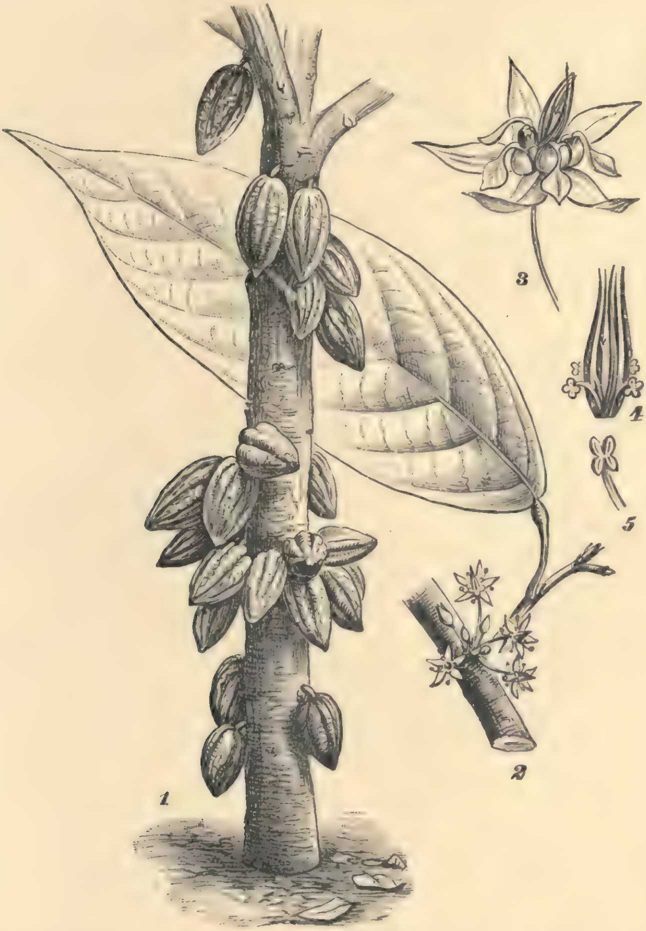


Fig. 677.—*Theobroma Cacao.* *1*, Stem bearing fruits. *2*, Flowering branch. *3*, Flower. *4*, Circle of stamens. *5*, Stamens from anterior side. (*3*, *4*, about nat. size; *5*, enlarged; *1*, *2*, greatly reduced.) ***OFFICIAL.***

downwards. The flowers are borne on the main stem or the older branches, and arise from dormant axillary buds (CAULIFLORY). Each petal is bulged out at the base, narrows considerably above this, and ends in an expanded tip. The form of the reddish flowers is thus somewhat urn-shaped with five radiating points. The pentalocular ovary has numerous ovules in each loculus. As the fruit develops, the soft tissue of the septa extends between the single seeds; the ripe fruit is thus unilocular and many-seeded. The seed-coat is filled by the embryo, which has two large, folded, brittle cotyledons. *Cola*

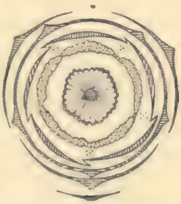


Fig. 678.—Malvaceae. Floral diagram (*Malva*).

acuminata and *C. vera*, natives of tropical Africa, yield the Kola nuts which are used in medicine.

OFFICIAL.—*Theobroma Cacao*, from which OLEUM THEOBROMATIS is obtained.

Family 3. **Malvaceae**.—Herbs or shrubs, frequently with palmately-lobed, stipulate leaves which in the young condition often have a velvety covering of stellate hairs. Flowers with an epicalyx, a gamosepalous calyx, and a corolla which is usually of considerable size and attractively coloured, and is contorted in the bud. Protandrous. Stamens united into a tube around the ovary; the free ends of the stamens, each of which bears a single reniform theca, project from the margin of the staminal tube. Pollen-grains with spiny exine (cf. Fig. 474). Carpels usually numerous. Fruit, a schizocarp or a capsule (Figs. 678-681).

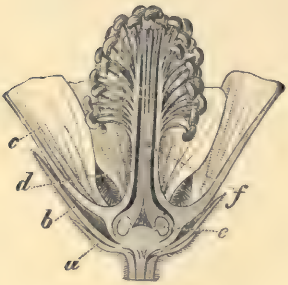


FIG. 679.—Flower of *Althaea officinalis*, cut through longitudinally. *a*, Outer; *b*, inner calyx; *c*, petals; *d*, androecium; *f*, pistil; *e*, ovule (magnified). (After BERG and SCHMIDT.)

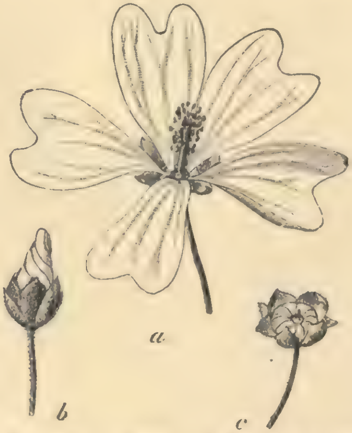


FIG. 680.—*Malva silvestris*. *a*, Flower; *b*, flower-bud; *c*, fruit (nat. size.)

IMPORTANT SUB-FAMILIES AND GENERA.—1. *Malveae*.—Schizocarps composed of numerous carpels arranged in a circle. *Malva*, with a number of British species (Fig. 680). Perennial herbs, with long-stalked, palmately-veined leaves. Flowers solitary or in small cymose inflorescences in the axils of leaves. Three, free segments of the epicalyx. Petals usually rose-coloured, deeply notched. In *Althaea* the whole plant is clothed with stellate hairs giving it a soft velvety appearance. Epicalyx of 6-9 segments united at the base.

2. *Hibisceae*.—Fruit, a capsule usually formed of five carpels with a corresponding number of loculi. *Hibiscus* is frequently cultivated as an ornamental plant. *Gossypium*, shrubs with three- to five-lobed leaves with long stalks. Flowers with a large epicalyx of three segments, which completely covers the calyx. Fruit of three to five carpels, loculicidal. Seed covered with long hairs which aid in its dispersion by the wind. When stripped from the seeds and cleaned these hairs

form cotton wool. The most important species of Cotton are *G. barbadense*, *G. arboreum*, *G. herbaceum* (Fig. 681).

OFFICIAL.—*Gossypium barbadense* and other species yield GOSSYPIUM.

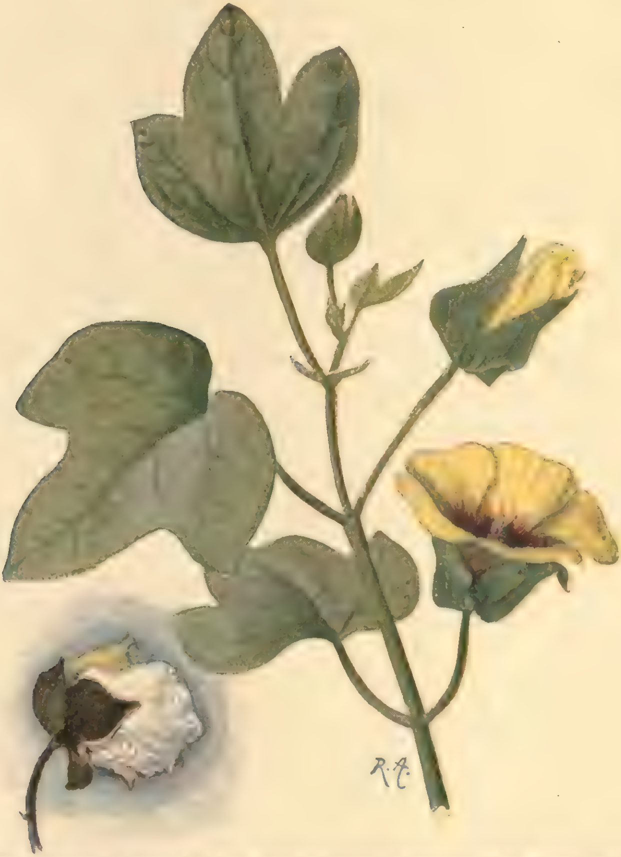


FIG. 681.—Flowering branch and open fruit of *Gossypium herbaceum* (½ nat. size). *OFFICIAL.*

Order 18. Cistiflorae

The plants belonging to this order are characterised by their usually regular, pentamerous flowers; the stamens are increased in number by chorisis, or when the separation of the branches is incomplete they form distinct bundles; the superior ovary is usually trimerous.

Family 1. **Ternströmiaceae.**—Herbs, shrubs, or trees, with alternate, simple, leathery leaves. Flowers regular; æstivation imbricate; sometimes with indistinct separation of calyx and corolla. Stamens numerous. Ovary septate. *Thea chinensis* (Fig. 682) is a small evergreen tree or shrub, native to southern China. The young leaves and tips of the shoots yield TEA after being fermented and dried. The tea-plant is cultivated on an extensive scale in China, Japan, and many tropical colonies. CAFFEINE is obtained from *Thea chinensis*. *Thea japonica*, the Camellia, is a favourite ornamental shrub.

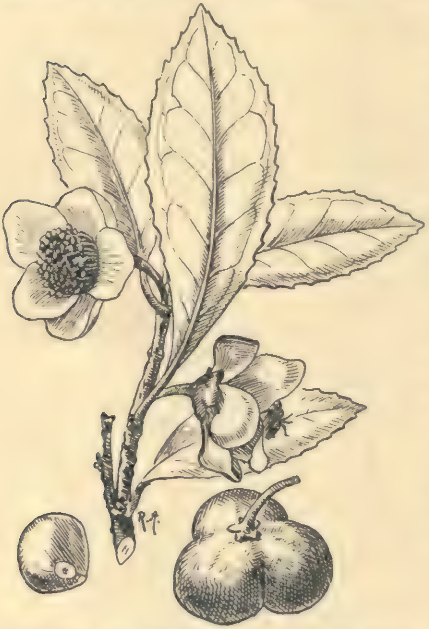


FIG. 682.—*Thea chinensis*. Flowering shoot (⅔ nat. size); fruit and seed.

Family 2. **Guttiferae.**—Herbs, shrubs, or trees with opposite, simple, entire leaves. Flowers sometimes diclinous. Stamens in bundles. Schizogenous intercellular spaces containing secretions in all parts of the plant. In Britain *Hypericum*, with a number of species; stamens in three or five bundles (Fig. 683). Oil glands apparent as translucent spots in the leaf-blade. *Garcinia Mangostana*, the Mangosteen, is one of the most esteemed fruit-trees of the Asiatic tropics.

OFFICIAL.—*Garcinia Hanburyi* is a tree of Farther India, with thick leathery leaves and diclinous flowers. The male flowers have numerous stamens seated on a short globular receptacle; the female flowers have an ovary composed of three to several carpels surmounted by a broadly peltate stigma. The red contents of the secretory organs which exudes on wounding the plant provides when dried, CAMBOGIA, Gamboge.

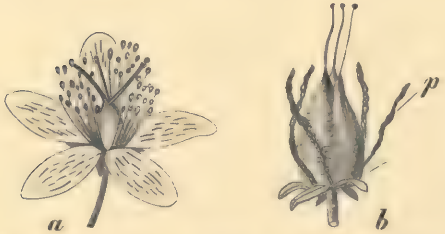


FIG. 683.—*Hypericum tetrapterum*. *a*, Flower, somewhat magnified; *b*, fruit; *p*, the dried, persistent petals. (× 2.)

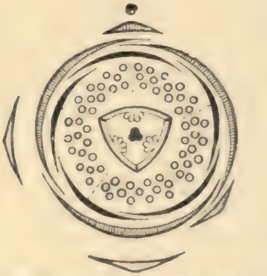


FIG. 684.—Floral diagram of *Helianthemum vulgare*. (Cistaceae.) (After EICHLER.)

Family 3. **Dipterocarpaceae.**—Contain secretory reservoirs. Characterised by the great enlargement of some or all the sepals after fertilisation. *Dryobalanops Camphora*, yields Borneo camphor. Dammar (33) is obtained from *Shorea Wiesneri*.

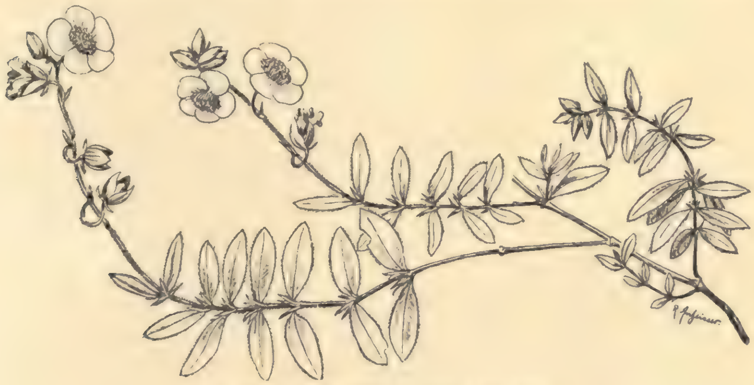


Fig. 685.—*Helianthemum vulgare* ($\frac{1}{2}$ nat. size).

Family 4. **Cistaceae.** — Perennial herbs or shrubs with opposite, simple, stipulate leaves. Pentamerous, regular flowers, with numerous stamens and three or five carpels united to form a unilocular or multilocular ovary with a single style. In Britain the Rock Rose (*Helianthemum vulgare*); the prostrate stem bears small elliptical, sessile leaves and racemes of bright yellow flowers (Figs. 684, 685). Many species of *Cistus* are characteristic shrubs of the type of vegetation of the Mediterranean region, known as the Maquis.

Family 5. **Violaceae.**

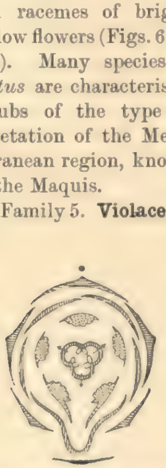


Fig. 686.—Floral diagram of *Viola*.

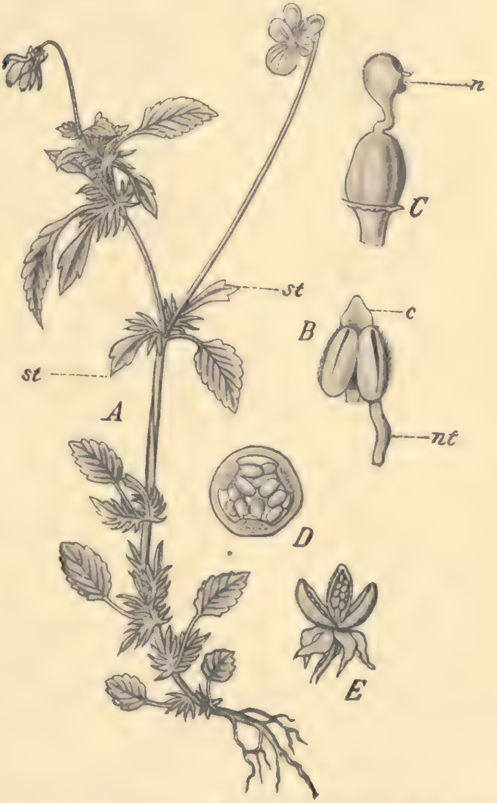


Fig. 687.—*Viola tricolor*. *A*, Entire plant (reduced); *st*, stipules. *B*, a stamen, enlarged; *c*, connective; *nt*, nectary. *C*, gynaeceum, enlarged; *n*, stigma. *D*, transverse section of ovary. *E*, fruit (nat. size).

—Herbs, shrubs or trees, usually with dorsiventral flowers with only five stamens. Ovary unilocular with a simple style. There are a number of species of *Viola* in Britain. The flowers have the anterior petal prolonged backwards as a spur, into which two nectar-secreting processes of the two anterior stamens project (Figs. 686, 687). Many kinds of Violet have, in addition to these conspicuous flowers adapted to insect pollination, inconspicuous, cleistogamous flowers which are self-fertilised (cf. p. 309). *Viola tricolor*, the Wild Pansy, has large pinnately-divided stipules hardly smaller than the leaf-blade itself.

Order 19. Passiflorinae

Flowers radial, perigynous or epigynous. Ovary of three carpels, unilocular, with parietal placentation ; usually three bifid stigmas.

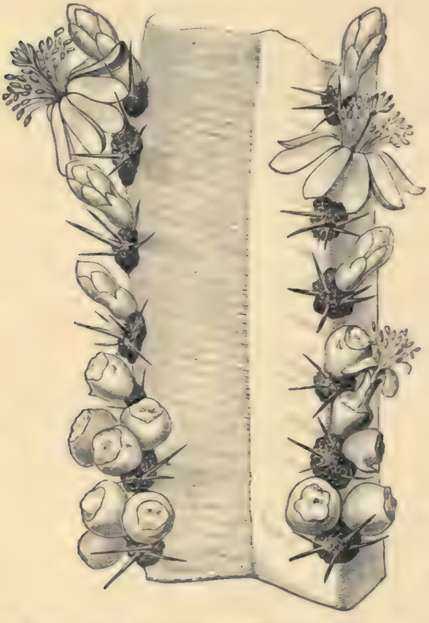


FIG. 688.—*Cereus geometrizans.* Two of the ribs or ridges of a five-ribbed stem bearing flowers and fruits (¾ nat. size).

Family **Passifloraceae.**—Plants climbing by means of tendrils. Flowers large, complicated by outgrowths from the floral axis (corona and disc). *Passiflora*, Passion Flowers ; ornamental plants from South America.

Family **Caricaceae.** — *Carica papaya*, the Papaw, has in its latex a ferment (papayotin) resembling pepsin. Tropical.

Family **Begoniaceae.** — Herbs with obliquely cordate leaves. Flowers unisexual. Ovary inferior. Mostly tropical. Many species of *Begonia* are in cultivation.

Order 20. Opuntinae (34)

Family **Cactaceae.**—For the most part leafless plants with succulent stems, natives of America. In size they range from very small to gigantic forms. Flowers hermaphrodite, actinomorphic, less commonly dorsiventral. Perianth of many members, spirally arranged and showing a gradual transition from the calyx to the corolla. Stamens and carpels numerous. Ovary inferior, unilocular, with numerous parietal placentas. Ovules with long stalks. Fruit, a berry, the succulent tissue being largely derived from the stalks of the seeds.

Peireskia and some species of *Opuntia* possess leaves. Other species of *Opuntia* have flattened branches. *Cereus, Echinocactus*, with longitudinal ridges on the stem ; *Mamillaria* has free projections (mamillæ). The numerous groups of spines on the shoots, ribs, or separate mamillæ correspond to axillary shoots, the subtending leaves of which are reduced while the leaves of the expanded axis of the axillary shoot are metamorphosed into spines (Fig. 688).

Cactaceae form a dominant constituent of the vegetation in the dry south-western regions of the United States and in Mexico. They are also widely distributed in the West Indies and South America. A similar habit is found in some Euphorbiaceae and Asclepiadaceae living under corresponding climatic conditions. There are numerous epiphytic Cactaceae, especially species of *Rhipsalis*, *Epiphyllum*, and *Phyllocactus*, which clothe the branches of trees and affect the general aspect of the vegetation.

Opuntia ficus indica has become naturalised in the Mediterranean region. The fruits of this species and of others of the genus are edible, and the plants are cultivated as fruit-trees. Some Cactaceae, such as *Anhalonium*, contain highly poisonous alkaloids and saponine. The Cochineal insect is grown upon species of *Opuntia* and *Nopalea* (*N. coccinellifera*).

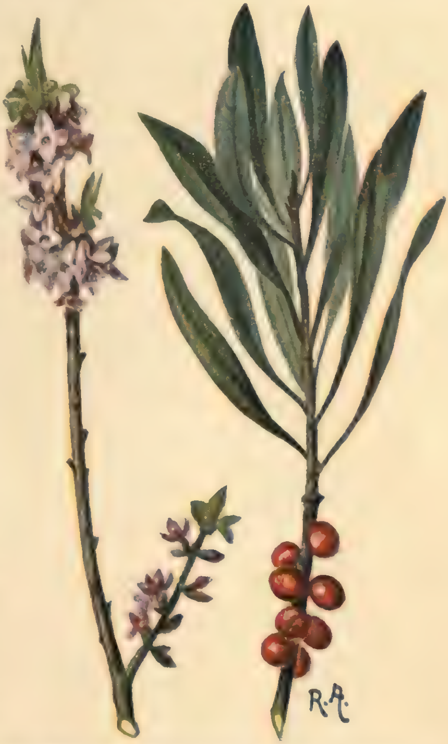


Fig. 689.—*Daphne Mezereum* (½ nat. size). *OFFICIAL* and *POISONOUS*.

Order 21. Thymelaëinae

Shrubs or trees, with simple, entire leaves, often closely crowded. Flowers perigynous, hermaphrodite, actinomorphic, tetramerous or pentamerous. Corolla often wanting. Stamens in one or two whorls. Carpel, one. Ovary with a single ovule.

Family 1. **Thymelaeaceae.**—Ovule pendulous. *Daphne Mezereum* (Fig. 689) is a poisonous shrub, possibly native to Britain, which flowers in February and March before the leaves appear. The flowers are rose-coloured, scented, tetramerous, and have no corolla. The leaves form a close tuft until the axis elongates. The fruit is a bright red berry. In the Alps and in the Mediterranean region there are numerous species of *Daphne*, all of which are poisonous.

OFFICIAL.—*Daphne Mezereum*, *D. Laureola*, and *D. Gnidium* yield MEZEREI CORTEX.

Family 2. **Elaeagnaceae.**—Ovule erect. *Hippophaë. Elaeagnus.* The leaves and young twigs are covered with shining peltate hairs.

Order 22. Myrtiflorae

Leaves opposite, simple, entire, exstipulate; flowers hermaphrodite, actinomorphic, tetramerous or pentamerous, hypogynous, or at most perigynous. Ovary septate. Increase in number of the stamens is frequent.

Family 1. **Lythraceae.**—*Lythrum salicaria.* Purple Loosestrife. K 6, C 6, A 6 + 6, G$\overline{(2)}$. Heterostyled with three forms of flower (cf. p. 311).

Family 2. **Melastomaceae.**—An exclusively tropical family, easily recognised by the beautifully shaped and regularly veined leaves. Favourite hothouse plants.

Family 3. **Onagraceae** (35).—K 4, C 4, A 4 + 4, G$\overline{(4)}$. Androecium obdiplostemonous. Ovary inferior (Figs. 690, 691).

More Important Genera.—*Epilobium*, Willow-herb, with numerous species; the fruit is a capsule, and the seeds have hairs serving for wind-dispersal. *Oenothera.* The power of mutating possessed by plants of this genus was recognised by de Vries and forms the experimental basis of his hypothesis of mutation. *Circaea*, Enchanter's Nightshade. *Trapa*, Water Nut. Many forms are in cultivation, for instance the species of *Fuchsia*, in which the calyx is petaloid. These plants are natives of America. Fruit, a berry.

Family 4. **Halorrhagidaceae** (35a).—Aquatic plants with small, inconspicuous flowers. *Myriophyllum. Hippuris.*

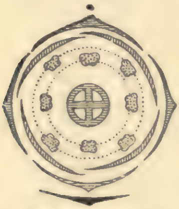


Fig. 690.—Floral diagram of *Oenothera* (Onagraceae).

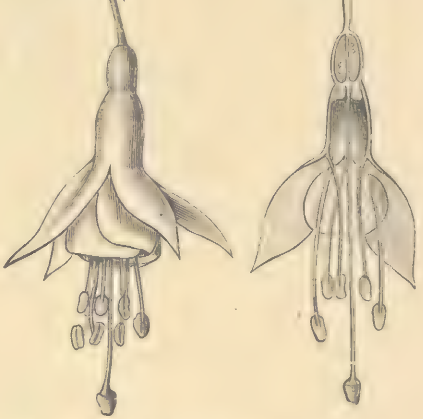


Fig. 691.—*Fuchsia globosa.* Flowers (nat. size).

Family 5. **Rhizophoraceae** (36).—Plants occurring in the Mangrove formation along tropical coasts, characterised by vivipary and the possession of stilt-roots or respiratory roots. These adaptations are related to the peculiarities of the situations in which the trees grow. *Rhizophora* (Fig. 692); *Bruguiera*; *Ceriops.*

Family 6. **Combretaceae.**—*Terminalia Chebula* yields MYROBALANS.

Family 7. **Myrtaceae.**—Evergreen shrubs or trees; leaves opposite, leathery, often aromatic. Flowers actinomorphic, tetramerous or pentamerous. Androecium of many stamens, which are often arranged in bundles which have originated by branching. Carpels two to many, united with the floral axis to form the inferior ovary. Fruit, usually a berry or a capsule.

Important Genera.—The Myrtle (*Myrtus communis*), which occurs in the Mediterranean region, is the only European species. Species of *Eucalyptus*, from

Australia, especially *E. globulus*, are commonly planted in Italy, on account of their rapid growth and useful timber. Young plants have opposite, sessile leaves, but older trees bear stalked, sickle-shaped leaves which hang vertically. The shadeless condition of the Australian forests formed by these trees, depends in part on this character, but is partly due to the distance apart of the individual trees. *E. amygdalina*, which reaches a height of 155 m. and a circumference of 30 m. at the base of the trunk, is one of the largest forest trees known. *Psidium guayava* and some species of *Jambosa* bear edible fruits; the former is especially valued. *Eugenia caryophyllata* (Moluccas) is of economic importance, its unopened flower-buds forming Cloves (Fig. 694). This tree is commonly cultivated in the tropics. It has a beautiful appearance when the terminal groups of flowers (which in bud

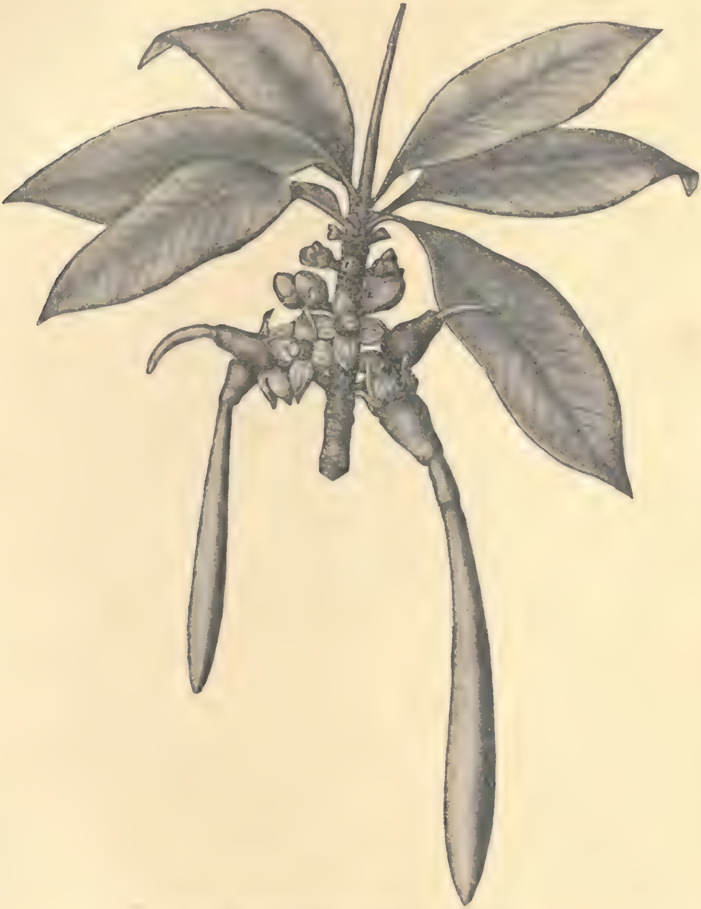


FIG. 692.—*Rhizophora conjugata* (¼ nat. size).

are of a bright red colour with four united, white petals and when opened exhibit numerous whitish stamens) are seen through the shining foliage composed of entire leaves. The corolla is thrown off when the flower opens. In Fig. 694 the inferior ovary, formed of two carpels, is also seen in longitudinal section.

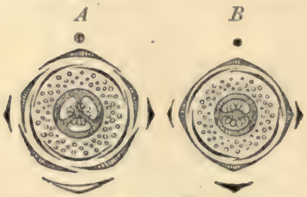


FIG. 693.—Floral diagrams of Myrtaceae. *A*, *Myrtus communis*; *B*, *Eugenia aromatica*. (After EICHLER.)

OFFICIAL. — *Eugenia caryophyllata* yields CARYOPHYLLUM, Cloves. PIMENTA, Allspice, from *Pimenta officinalis*. OLEUM CAJAPUTI from *Melaleuca leucadendron*, a tree of less height but resembling the Eucalyptus trees; it is cultivated in the Moluccas (Buru) for the sake of the oil it yields; its specific name refers to the white colour of the bark. OLEUM EUCALYPTI and EUCALYPTI GUMMI from *Eucalyptus globulus* and other species.

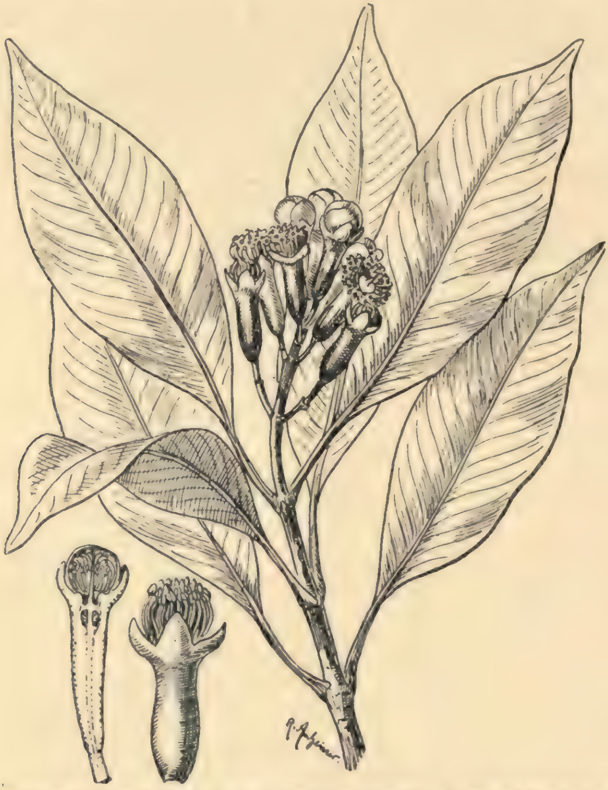


FIG. 694.—*Eugenia caryophyllata* ($\frac{2}{3}$ nat. size). Flowering branch. A bud cut in half and an opened flower (about nat. size). *OFFICIAL.*

Family 8. **Punicaceae.**—Single genus *Punica*. *Punica granatum* is a tree originally introduced from the East and now largely cultivated in the Mediterranean region on account of its acid refreshing fruits known as Pomegranates (Fig. 695). Leaves small, entire. Flower with a stiff, red calyx, an indefinite number of petals, and numerous stamens; the 7-14 carpels are arranged in two tiers, the upper of which corresponds in number to the sepals, the lower to the half of this (Fig. 696). Fruit enclosed by a leathery pericarp with numerous seeds in the loculi of both tiers. The external layers of the seed-coat become succulent and form the edible portion of the fruit.

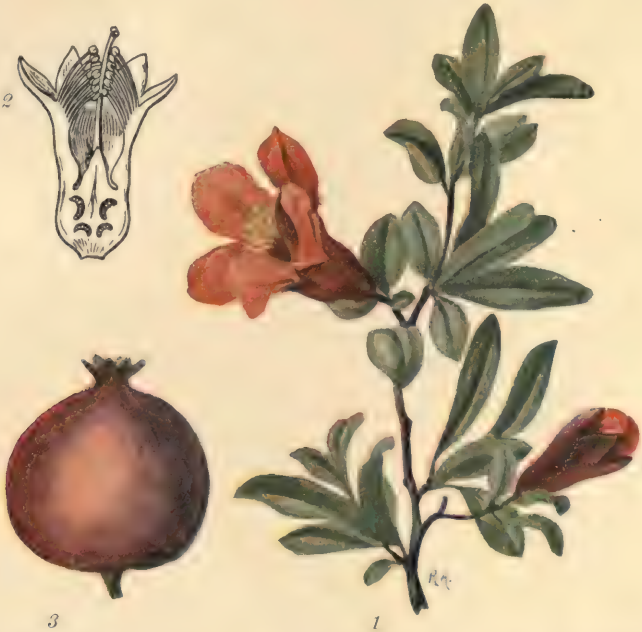


Fig. 695.—*Punica granatum* (½ nat. size). *1*, Branch bearing a flower and a bud. *2*, Flower in longitudinal section. *3*, Fruit. (See text.) *Official.*

Official. — *Punica granatum*, from which **granati cortex** is obtained.

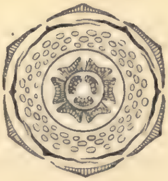


Fig. 696.—Floral diagram of *Punica granatum*. (After Eichler.)

Order 23. Umbelliflorae

Inflorescence as a rule an umbel. Flowers hermaphrodite, actinomorphic, tetramerous or more usually pentamerous; calyx only slightly developed; a single whorl of stamens and an inferior bilocular ovary, the upper surface of which forms the nectary.

Carpels two. A single pendulous ovule in each loculus. Seed with abundant endosperm.

Family 1. **Cornaceae.**—For the most part shrubs or small trees, rarely herbs. Leaves simple, usually decussate. K4, C4, A4, G (2). Fruit, a berry or a drupe.

Cornus mas, the Cornelian Cherry (Fig. 697), expands its umbels of yellow flowers before the leaves appear. Each umbel is subtended by four bracts. The inflorescences for the succeeding year are already present in the axils of the leaves by the time the fruit is ripe. In Britain two species occur; *C. sanguinea*, the Dogwood, and *C. suecica*, an arctic and alpine plant which reaches its southern limit in Germany.

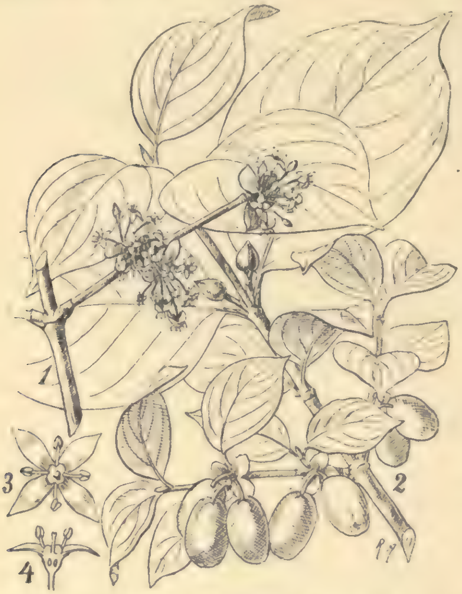


FIG. 697.—*Cornus mas* (½ nat. size). *1*, Flowering twig. *2*, Twig with fruits. *3*, Flower seen from above. *4*, Flower in longitudinal section. (*3*, *4*, enlarged.)

Family 2. **Araliaceae.**—Trees or shrubs with alternate leaves, which are often of considerable size and simple, lobed, or compound in shape. Floral formula, K5, C5, A5, G$(\bar{5})$. Flowers in umbels or heads, often further grouped in a panicle-like inflorescence. The carpels vary in number from 2-5 or more.

In Britain the only representative of the family is the Ivy (*Hedera Helix*), a root-climber. The proper elliptical leaf form reappears on the orthotropous shoots of older plants, which in late summer or autumn bear the flowers. The leaves of the creeping or climbing plagiotropous shoots are lobed and usually have shorter stalks (Fig. 698). Calyx with five, pointed sepals corresponding to the five ribs on the inferior ovary. The corolla is greenish in tint; the large disc on the upper surface of the ovary attracts the visits of bees. The fruits ripen during the winter and become blackish-blue berries; these are eaten by birds and in this way the seeds are distributed.

Family 3. **Umbelliferae.**—Herbaceous plants sometimes of large size. The stem, which has hollow internodes and enlarged nodes, bears alternate leaves; these completely encircle the stem with their sheathing base, which is often of large size. The leaves are only rarely simple; usually they are highly compound. Inflorescence terminal, frequently overtopped by the next younger lateral shoot. It is an umbel, or more frequently a compound umbel, the bracts forming the involucre and partial involucres, or an involucre may be wanting. Flowers white, greenish, or yellow; other colours are

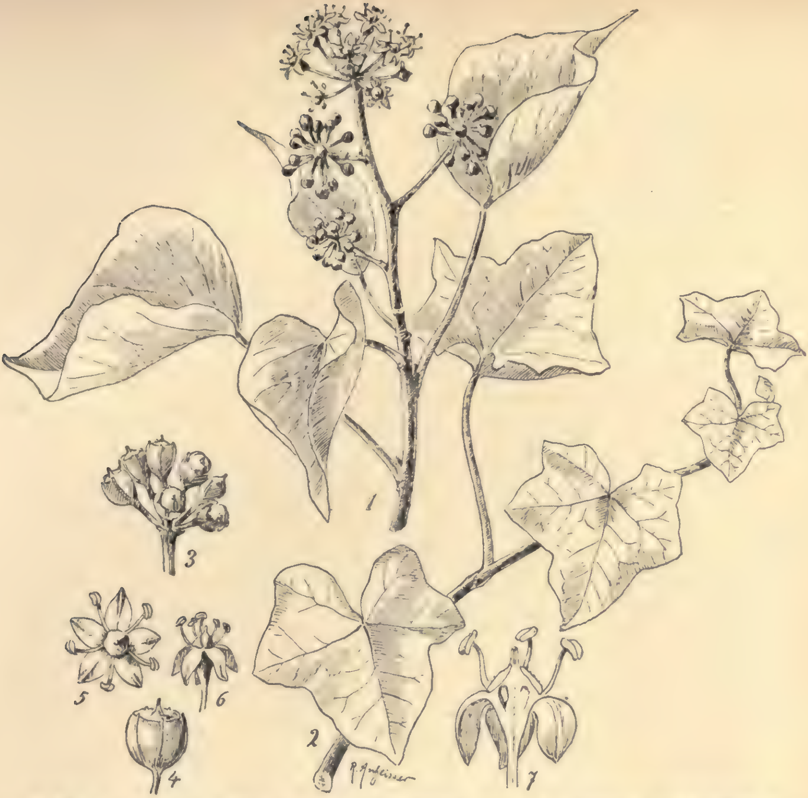


FIG. 698.—*Hedera helix* (½ nat. size). *1*, Erect flowering shoot. *2*, Creeping shoot showing the distinct form of the leaves. *3*, Fruits. *4*, Single fruit. *5*, Flower from above. *6*, Flower from the side. *7*, Flower cut through longitudinally. (*4-7* enlarged.) ***POISONOUS.***

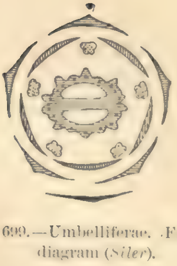


FIG. 699.—Umbelliferae. Floral diagram (*Siler*).

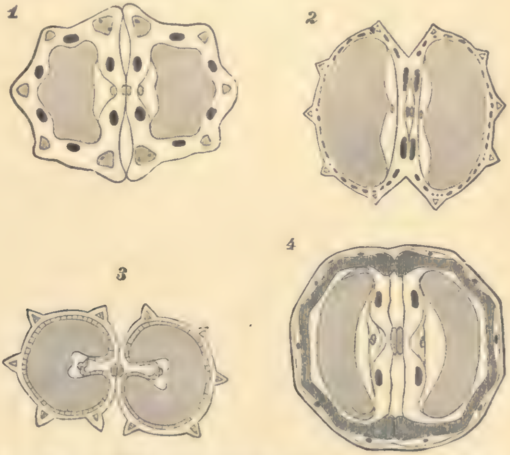


FIG. 700.—Fruits of Umbelliferae in cross section. *1*, *Foeniculum officinale*. *2*, *Pimpinella Anisum*. *3*, *Conium maculatum*. *4*, *Coriandrum sativum* (*4* modified after a figure by DRUDE).

rare. K 5, C 5, A 5, G $(\bar{2})$. The sepals are usually represented by short teeth. The flowers at the circumference of the compound umbel sometimes become zygomorphic by the enlargement of the outwardly directed petals. Ovary always bi-carpellary and bilocular; in each loculus a single ovule which hangs from the medium septum with its micropyle directed upwards and outwards. The upper surface of the carpels is occupied by a swollen, nectar-secreting disc continuing into the longer or shorter styles, which terminate in spherical stigmas. Fruit a schizocarp, splitting in the plane of the septum into two partial fruits or mericarps. In many cases the latter remain for a time attached to the carpophore, which originates from the central

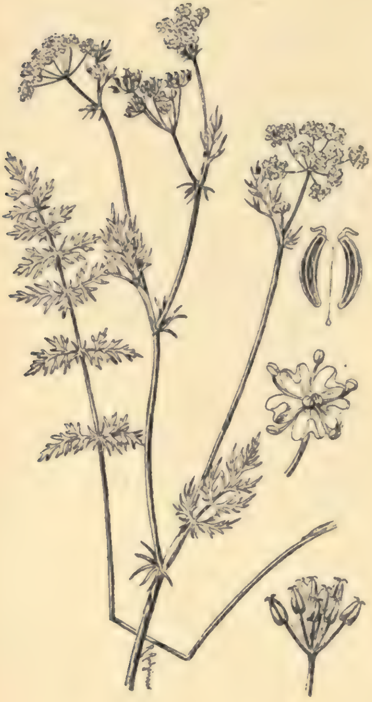


FIG. 701.—*Carum carvi* (½ nat. size). Inflorescence bearing fruits. Single flower, and carpophore bearing the mericarps (enlarged). ***OFFICIAL.***

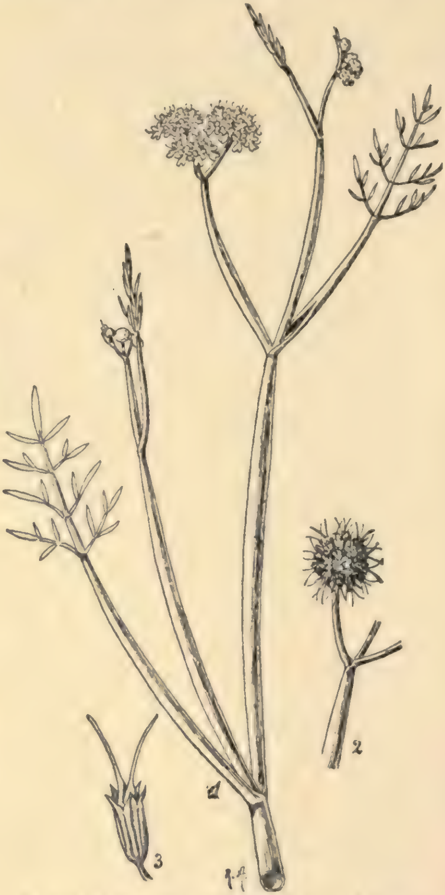


FIG. 702.—*1, Oenanthe fistulosa* (½ nat. size). *2.* Group of fruits. *3,* Single fruit (enlarged). ***POISONOUS.***

portion of the septum ; this separates from the rest of the septum and bears the mericarps hanging from its upper forked end (Figs. 699-706).

For systematic purposes the fruits are of great importance. Each half of the fruit has five ribs, beneath which the vascular bundles lie. The marginal ribs of each partial fruit frequently lie close together at the septum or they may be distinct ; they may resemble the three dorsal ribs or differ more or less from them. Between the five primary ribs four secondary ribs are sometimes present. Usually furrows (valleculæ) occur between the ridges, and beneath each furrow a large oil duct (vitta) is found, extending the whole length of the fruit. On either side of the carpophore a similar oil duct is present in the septum, so that each mericarp has six of these vittæ (Fig. 700). In some species additional small ducts are present. The form of the fruit as seen in a cross section differs according to whether the diameter is greater in the plane of the septum or at right angles to this. The character of the marginal and dorsal ridges and the presence or absence of secondary ridges or vittæ serve to distinguish the fruits, and are indispensable aids in determining the species. Since many of the fruits are employed in medicine or as spices, while others are poisonous, their distinction becomes a matter of importance. The endosperm of the seeds contains a fatty oil as reserve material.

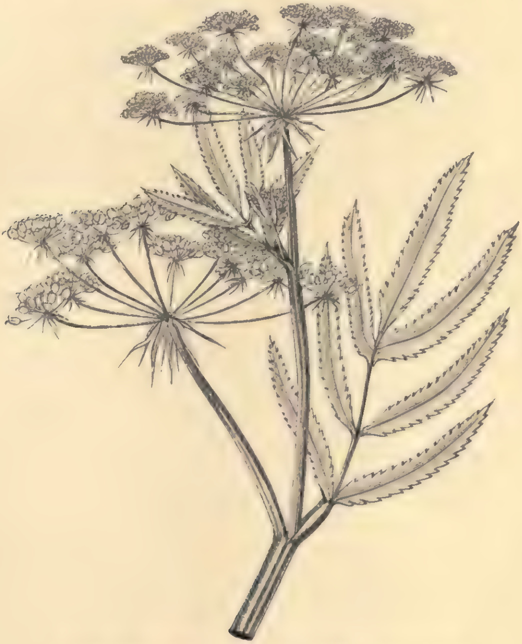


FIG. 703.—*Sium latifolium* (½ nat. size). *POISONOUS.*

The most recent revision of the family is by Drude in Engler-Prantl, *Nat. Pflanzenfam.* ; an older useful division is founded on the shape of the endosperm.

1. *Orthospermae.*—The endosperm flat or slightly convex on the ventral side,

i.e. on the side towards the plane of junction of the two mericarps (Fig. 700, 1, 2). The majority of the species belong to this group. *Hydrocotyle* is a creeping plant growing in marshy places with entire, peltate leaves and simple umbels. *Sanicula* and *Astrantia* have simple umbels, which in the latter are surrounded by a petaloid involucre. In *Eryngium* the plant is usually spiny and bears simple umbels, which approach closely to being capitula; the involucral leaves are often coloured. *Bupleurum* has entire leaves. *Pimpinella*, Burnet-Saxifrage. *P. Anisum*, Anise, is an annual plant, the seedlings of which exhibit increasing subdivision of the lamina in successive leaves. *Carum Carvi*, Carroway, has long been cultivated (Fig. 701); leaves bipinnate, the lowest pinnæ resembling stipules. The large lower pinnules are usually placed horizontally on the vertical rhachis of the leaf; the terminal pinnules are simple and linear. The termina-

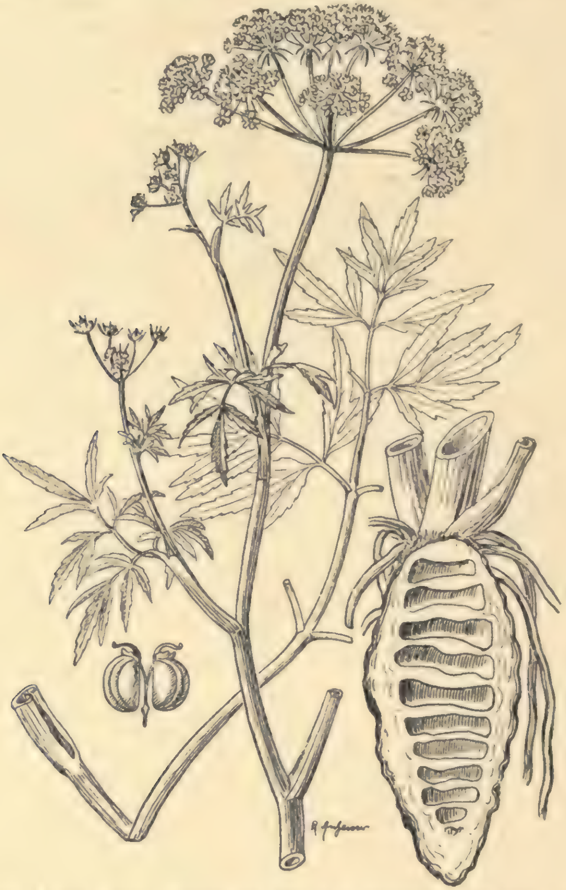


FIG. 704.—*Cicuta virosa*. Rhizome cut through longitudinally (½ nat. size). Fruit (enlarged). POISONOUS.

umbel, the flowers of which open first, is overtopped by the lateral umbels arising from the leaf-axils. Biennial. *Carum Bulbocastanum* has a perennial, tuberous rhizome; its seedlings have only one cotyledon. *Foeniculum* (Fennel) and *Levisticum* (Lovage) have yellow flowers. *Petroselinum* (Parsley), *Pastinaca* (Parsnip), *Daucus* (Carrot), *Apium* (Celery), and *Anethum* (Dill), are used as vegetables. *Cicuta* (Water-Hemlock, Fig. 704), *Sium* (Water-Parsnip, Fig. 703), *Oenanthe* (Fig. 702), and *Berula*, are marsh- or water-plants. *Aethusa cynapium* (Fool's Parsley, Fig. 705) has the ribs of the fruit keeled; umbels with three elongated, linear, involucral leaves directed outwards. All the last-named plants are poisonous. *Archangelica officinalis* is a conspicuous plant reaching a height of 2 metres, with large, bipinnate leaves provided with saccate, sheathing bases; the greenish flowers are markedly protandrous, the styles and stigmas only developing after the stamens have fallen. In *Carum*, *Oenanthe*, *Cicuta*, and *Heracleum*, and notably in the large species of *Ferula*, the flowers become polygamous or of separate sexes by abortion of stamens or carpels; sometimes the plants become diœcious. The ovary is completely wanting in the male flowers.

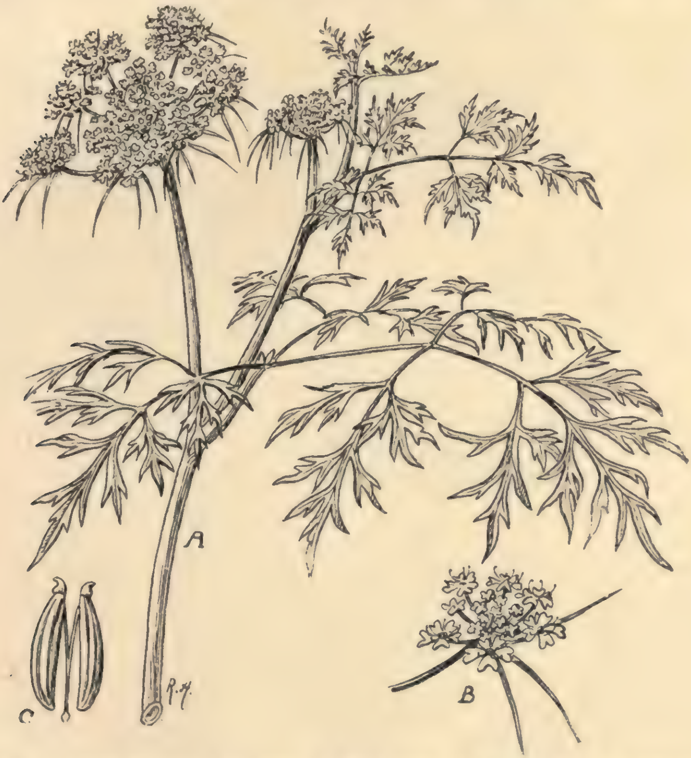


FIG. 705.—*Aethusa cynapium* ($\frac{2}{3}$ nat. size). *B*, Single umbel. *C*, Fruit (enlarged). *POISONOUS.*

2. *Campylospermae.*—The ventral side of the endosperm is traversed by a longitudinal groove (Fig. 700, 3). *Scandix*, *Anthriscus* (Beaked Parsley), *Chaero-*

phyllum (Chervil). *Conium maculatum*, the Hemlock, is a biennial plant often of considerable height ; it is completely glabrous, the stem and leaf-stalks often with purple spots ; leaves dull green, bi- to tri-pinnate. The ultimate segments end in a small, colourless, bristle-like tip. Fruit with wavy, crenate ridges and without oil-ducts in the valleculæ. The whole plant has a peculiar, unpleasant odour (Fig. 706).

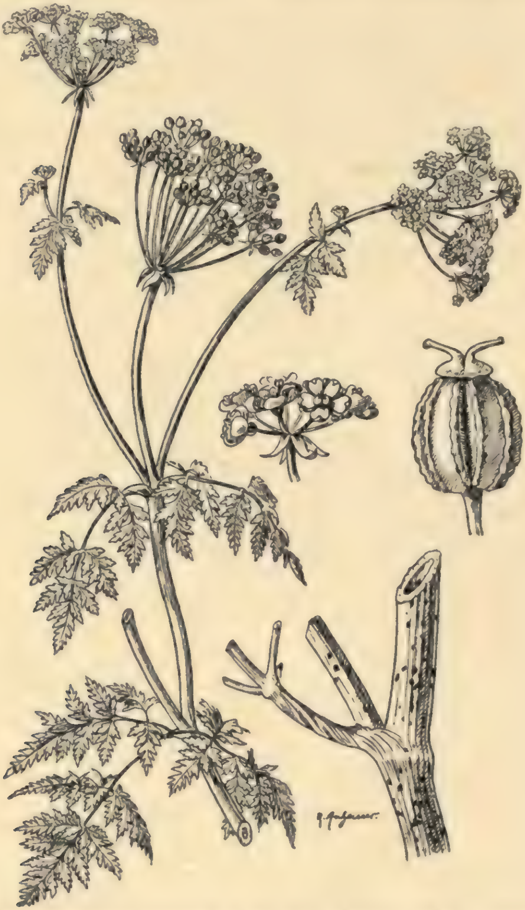


FIG. 706.—*Conium maculatum* (½ nat. size). *OFFICIAL* and *POISONOUS.*

3. *Coelospermae.*—The ventral side of the endosperm is concave (Fig. 700, 4). *Coriandrum sativum* is an annual plant ; flowers zygomorphic owing to the enlargement of the sepals and petals at the periphery of the umbel. Fruit spherical ; mericarps closely united, with ill-marked primary ridges and somewhat more distinct secondary ridges.

OFFICIAL.—*Conium maculatum* yields CONII FOLIA and CONII FRUCTUS. *Ferula foetida* (Persia), ASAFETIDA. *F. galbaniflua* and other species (Persia), GALBANUM.

Dorema Ammoniacum (Persia), AMMONIACUM. *Pimpinella anisum*, FRUCTUS ANISI. *Coriandrum sativum*, CORIANDRI FRUCTUS. *Foeniculum capillaceum*, FOENICULI FRUCTUS. *Carum carvi*, CARUI FRUCTUS. *Anethum* (*Peucedanum*) *graveolens*, ANETHI FRUCTUS. *Ferula sumbul*, SUMBUL RADIX.

Order 24. Hysterophyta

This order provisionally groups together a number of plants which are for the most part parasitic. The several families show no close relationship to one another or to other families.

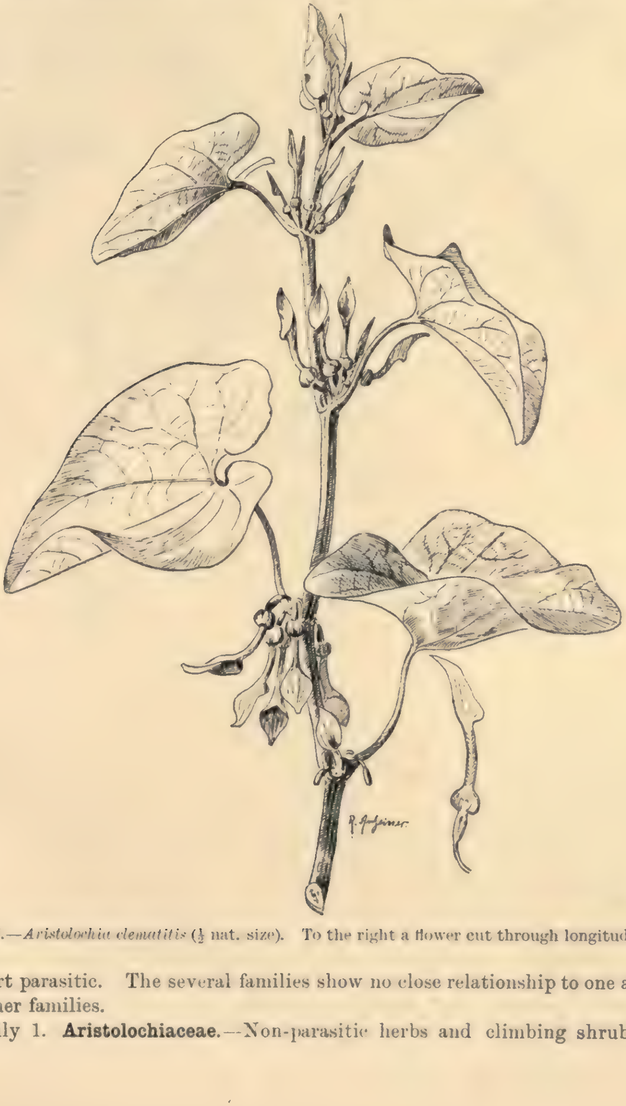


FIG. 707.—*Aristolochia clematitis* (½ nat. size). To the right a flower cut through longitudinally.

Family 1. **Aristolochiaceae.**—Non-parasitic herbs and climbing shrubs with simple, cordate leaves. Flowers with simple, gamophyllous perianth. Androecium and gynaeceum united to form a gynostemium. P3, A6 + 6. G(6). Inferior, septate ovary. Fruit a capsule.

Asarum europaeum occurs in Britain; flowers actinomorphic. *Aristolochia clematitis* (Fig. 707) has zygomorphic, protogynous flowers which are pollinated by small insects (cf. Fig. 243, p. 312). An erect herb with large, alternate leaves, bearing the numerous flowers in their axils.

Family 2. **Santalaceae** (37).—Green plants growing in the soil and parasitic on the roots of other plants from which their haustoria obtain nutrient materials. In Britain, *Thesium*.

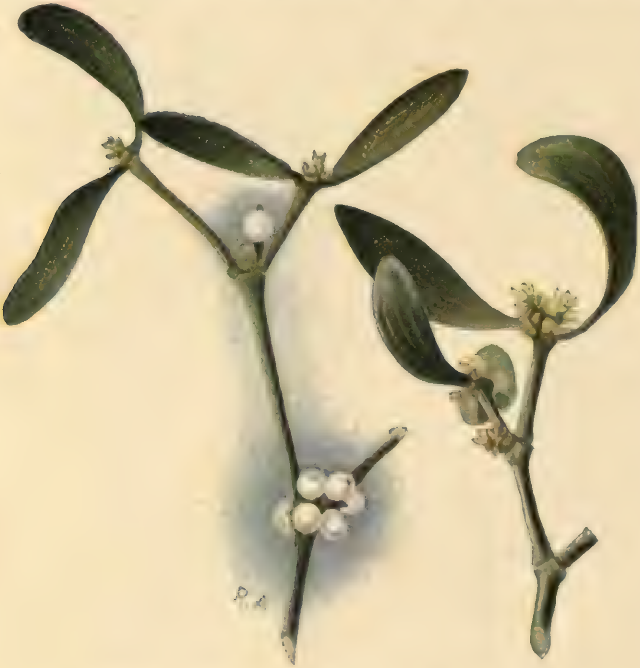


Fig. 708.—*Viscum album*. With flowers and fruits. (½ nat. size.)

OFFICIAL.—*Santalum album*, the wood of which when distilled yields OLEUM SANTALI. The wood is also of economic value.

Family 3. **Loranthaceae** (38).—Leafy, parasitic shrubs, living on the branches of trees. They are most abundant in the tropics, and, for instance in South America, add to the beauty of the forest by their brightly coloured flowers.

Loranthus europaeus, on Oaks in Europe. In Britain *Viscum album* (Fig. 708), the Mistletoe, occurs as an evergreen parasite on a number of trees. It has opposite, obovate leaves. Stem swollen at the nodes. The inconspicuous flowers open in early spring; they are diclinous and diœcious, usually bimerous, and are borne in five-flowered dichasia. The white berries ripen during the winter (December to March) and are eaten by birds. By means of a viscid layer of the pericarp they adhere, together with the seeds, to branches against which the birds rub their beaks. The root on germination forms an expanded, attaching disc. From the centre of this a sucker, which has no root-cap, penetrates the rind of the branch as far as the wood. From the base of this lateral roots arise, which grow in the rind giving off secondary suckers. As the wood of the host grows in thickness year by year, the tips of the suckers become embedded in the new wood. Their tips become converted into permanent tissue, while further growth in length is effected by a zone corresponding in position to the cambium of the host plant.

Family 4. **Rafflesiaceae** (39). Family 5. **Balanophoraceae** (40).—The plants belonging to these families are almost all tropical. They are parasitic, without chlorophyll, and with their vegetative organs reduced to haustoria. They have sometimes very large flowers (*Rafflesia*) or large inflorescences bearing numerous small flowers.

Rafflesia Arnoldi (Sumatra) has the largest of all known flowers, which attain a diameter of 1 metre. Many species of *Balanophora* are apogamous.

Series II. Sympetalae (15)

Perianth differentiated into calyx and corolla. Corolla gamopetalous. Flowers usually pentamerous, always cyclic. Two groups of Sympetalae can be distinguished. A. *Pentacyclicae.* Flowers with five regularly alternating whorls. K5, C(5), A5 + 5, G(5). B. *Tetracyclicae.* Flowers, by omission of the inner whorl of stamens, no trace of which persists, composed of four regularly alternating whorls. K5, C(5), A5, G(5) or more commonly G(2) by reduction in the number of carpels.

A. PENTACYCLICAE

Order 1. Ericinae (41)

Plants with actinomorphic flowers; androecium obdiplostemonous; stamens not adherent to the corolla. Pollen-sacs with an "exothecium"; pollen-grains frequently cohering in tetrads. Ovary, as a rule superior, multilocular.

Family 1. **Ericaceae.**—Evergreen, shrubby plants with small, often needle-shaped leaves. Anthers opening by pores or splits, frequently provided with horn-like appendages, on which account the group is also termed Bicornes. Fruit, a capsule, berry, or drupe. Seeds with a well-developed embryo and abundant endosperm (Figs. 709, 710).

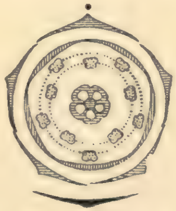


FIG. 709.—Floral diagram of *Vaccinium* (Ericaceae).

IMPORTANT SUB-FAMILIES AND GENERA.—A. With a superior ovary: 1. *Ericeae.* K4, C(4), A4+4, G(4). Corolla persistent. *Erica*, calyx shorter than the corolla, includes some British species (*E. Tetralix*) and many native to the Mediterranean region and the Cape. *Calluna*, calyx longer than the corolla. *C. vulgaris*, Heather or Ling, occurs on both dry and wet soils in western Europe. It ascends into alpine regions, and by itself or in association with a few other plants covers extensive tracts of country known as heaths or moors. 2. *Arbuteae.* Flowers pentamerous. Corolla deciduous. *Andromeda* occurs on moors in the northern hemisphere; fruit, a capsule. *Arctostaphylos Uva ursi*, circumpolar, in similar localities, has small, entire, leathery leaves. Fruit, a five-seeded drupe (Fig. 710). 3. *Rhodoreae.* Corolla deciduous. Capsule septicidal. *Rhododendron*, Alpine Rose. There are a few European species; many forms, especially Asiatic species, are cultivated as ornamental shrubs. *Ledum palustre* is a poisonous, evergreen shrub, occurring on moors in Europe: leaves rolled round at the margins; beautiful white umbels of flowers. Corolla polypetalous, star-shaped.

B. Ovary inferior: *Vaccineae.* *Vaccinium myrtillus*, Blaeberry, is a low, deciduous, shrubby plant. *V. vitis idaea*, Cowberry, is evergreen, and together with the preceding species is found in hilly regions.

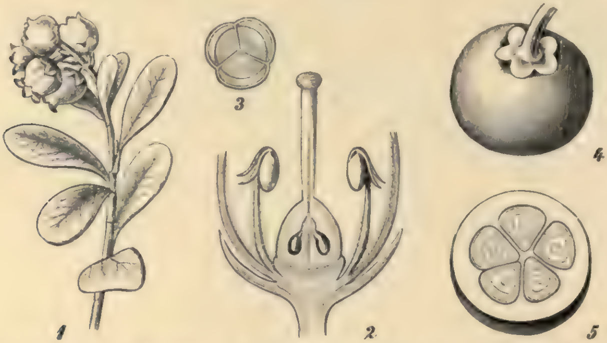


FIG. 710.—*Arctostaphylos Uva ursi.* *1*, Flowering branch; *2*, flowers in longitudinal section; *3*, pollen-grains; *4*, fruit; *5*, fruit in transverse section. (After BERG and SCHMIDT.) *OFFICIAL.*

OFFICIAL.—*Arctostaphylos Uva ursi* yields UVAE URSI FOLIA.

Family 2. **Pyrolaceae.**—Perennial, sometimes evergreen, herbaceous plants. Corolla often polypetalous. Seeds very small; embryo composed of only a few cells. *Pyrola*, several British species, with the flowers solitary or in racemes. *Monotropa* is a saprophyte devoid of chlorophyll. *M. hypopitys*, Bird's Nest, occurs rarely in woods, has a yellowish, succulent stem, bearing scale leaves below and ending in a racemose inflorescence with a few flowers.

Order 2. Diospyrinae

Actinomorphic, usually pentamerous flowers with a diplostemonous androecium. Antisepalous stamens frequently reduced. The **Sapotaceae** is a tropical family; the plants contain latex. Species of *Palaquium* and *Payena* from the Malayan Archipelago are the trees from which gutta-percha is obtained. Flowers hexamerous (Fig. 711). Balata is obtained from *Mimusops*; trees found throughout the tropics.

Ebenaceae.—*Diospyros Kaki* is a Japanese fruit tree; *D. Ebenum*, ebony.

Styracaceae.—The origin of Benzoin (BENZOINUM), an official resin, from *Styrax Benzoin*, though generally assumed, is open to doubt.

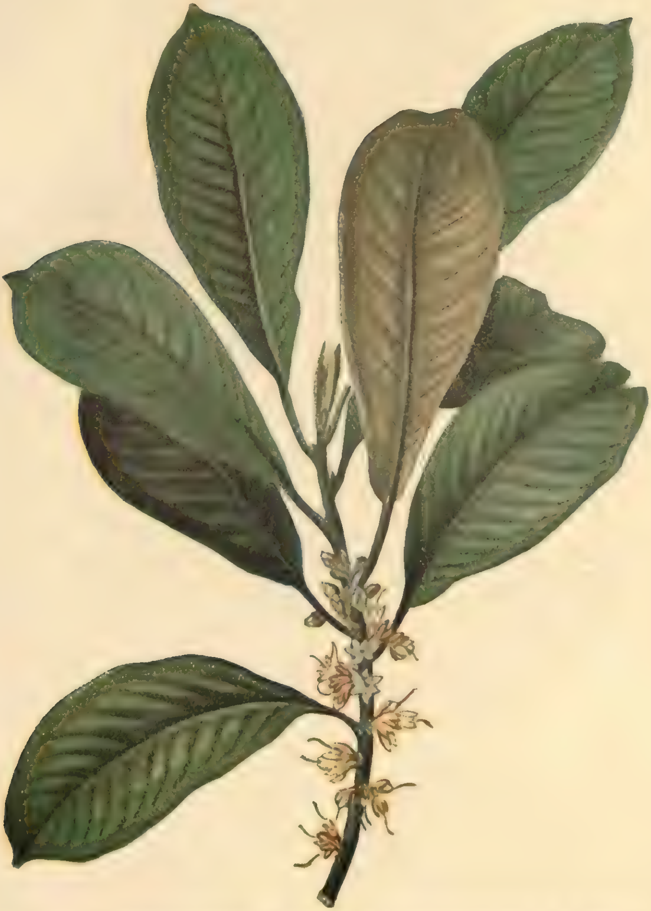


FIG. 711.—*Palaquium Gutta.* ($\frac{1}{2}$ nat. size. After SCHUMANN and A. MEYER.)

Order 3. Primulinae

Flowers sympetalous, actinomorphic with only one whorl of stamens; the latter are antipetalous, and are adherent to the corolla. Ovary unilocular, superior, with a free-central placenta. K 5, C(5), A 5, G(5).

Family 1. **Primulaceae**, Herbs, often with conspicuous flowers. Calyx green. Style, unbranched. Numerous ovules. Fruit, a capsule (Figs. 712-714).

IMPORTANT GENERA.—*Primula*, with several British species. Herbs with rosettes of leaves. Flowers solitary or in umbellate inflorescences. The capsules open by five teeth at the summit. Commonly grown as ornamental plants. *Anagallis*, capsule opens by a lid (pyxidium). Stem prostrate with leaves in decussate pairs (Fig. 714). *Lysimachia*, large herbaceous plants, with erect or creeping stems and decussate leaves. *Cyclamen* (42), flowers bent back on long stalks; tips of the petals bent back. Many species and hybrids are in cultivation. *C. europaeum*, the Alpine Violet (Fig. 713), is a herbaceous plant found in the Alps; the somewhat fleshy leaves have long stalks, and are borne on a large perennial tuber, which originates from the hypocotyl of the seedling. The stalks of the fruits become spirally rolled.

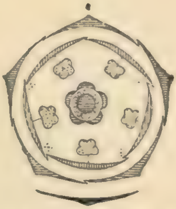


FIG. 712.—Primulaceae. Floral diagram (*Primula*).

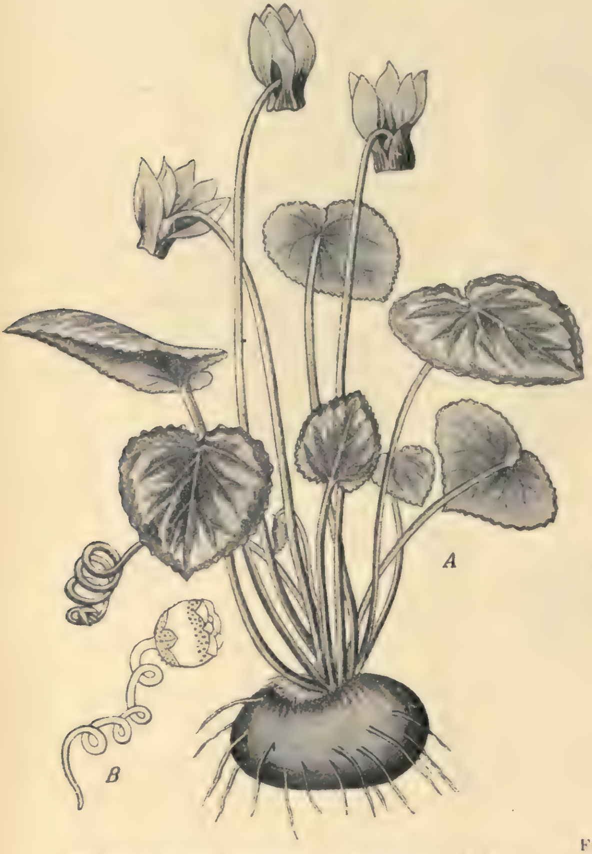


FIG. 713.—*Cyclamen europaeum*. *A*, entire plant; *B*, fruit. (After REICHENBACH.) *POISONOUS.*

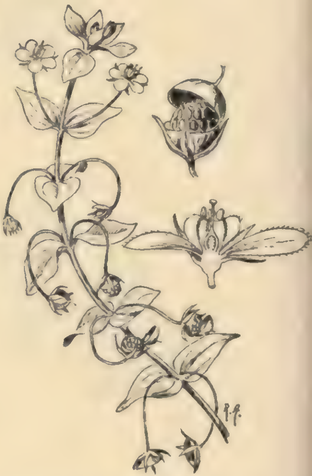


FIG. 714.—*Anagallis arvensis* (½ nat. size). Longitudinal section of flower and capsule at dehiscence (enlarged).

POISONOUS.—The tubers of *Cyclamen europaeum*, though harmless when cooked, are poisonous in the fresh state. *Anagallis* is slightly poisonous. *Primula obconica* (and *P. sinensis*) secrete in their glandular hairs certain substances which frequently give rise to rashes and to inflammation of the eyes of those handling the plants.

Family 2. **Plumbaginaceae.**—Herbs with a dry, membranous, but often brightly coloured calyx. Style branched. The ovary contains a single ovule. Species of *Armeria* and *Statice* are common plants of salt marshes.

B. TETRACYCLICAE

Order 4. Contortae

Plants with decussate, usually simple leaves and actinomorphic flowers, the corolla of which is often contorted in the bud. Stamens epipetalous. Ovary of two carpels, superior.

Family 1. **Oleaceae.**—Shrubs or trees without stipules. Flowers tetramerous, but with only two stamens. K 4, C(4), A 2, G$(\underline{2})$. Corolla with valvular or imbricate æstivation. Ovary bilocular; two ovules in each loculus (Fig. 715).

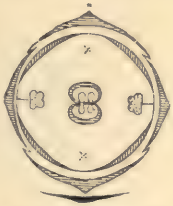


FIG. 715.—Oleaceae. Floral diagram (*Syringa*).

IMPORTANT GENERA.—*Olea europea*, the Olive (⁴³), a native of the Mediterranean region and of western Asia, where also it is cultivated. It is a tree with a poorly developed crown of slender pendulous branches bearing lanceolate, simple, entire leaves, which are dark green above, greyish green beneath. The flowers are borne in axillary racemes or panicles. The fruit is a drupe, both the succulent exocarp and the endosperm of which contain a fatty oil (Figs. 717-719). *Ligustrum vulgare*, the Privet. *Jasminum* and *Syringa* (Fig. 715) are grown as flowering shrubs. *Fraxinus*, the Ash, has imparipinnate leaves; *F. excelsior* has apetalous, anemophilous flowers, which appear before the leaves. *F. ornus*, the Flowering Ash, has a double perianth and is entomophilous; it is polygamous, having hermaphrodite flowers as well as female flowers with black, sterile anthers; the corolla is divided to the base (Fig. 716).

OFFICIAL.—*Olea europea* yields OLEUM OLIVAE.

Family 2. **Loganiaceae.**—Herbs, shrubs, or trees with stipulate leaves. K 5, C(5), A 5, G$(\underline{2})$. Tropical. Species of *Strychnos*, which are trees or lianes climbing by means of hook-tendrils, yield the arrow poison as well as the well-known Curare of South America, and that used by the Malays.

OFFICIAL.—*Strychnos nux vomica* is a small tree or shrub of southern Asia, the fruits of which are berries with a firm rind; in the succulent pulp a small number of erect, circular, disc-shaped seeds are embedded (Fig. 720). It yields NUX VOMICA and STRYCHNINA. GELSEMII RADIX is obtained from *Gelsemium nitidum*, which is a native of the south of North America.

Family 3. **Gentianaceae.** — Herbs, with exstipulate leaves. Corolla contorted in the bud (Fig. 721). The two carpels are united to form a unilocular ovary. Ovules numerous.

BRITISH GENERA.—*Gentiana* (⁴⁴) is a genus with numerous species. Plants of larger or smaller size, especially abundant in the Alps. Flowers brightly coloured.

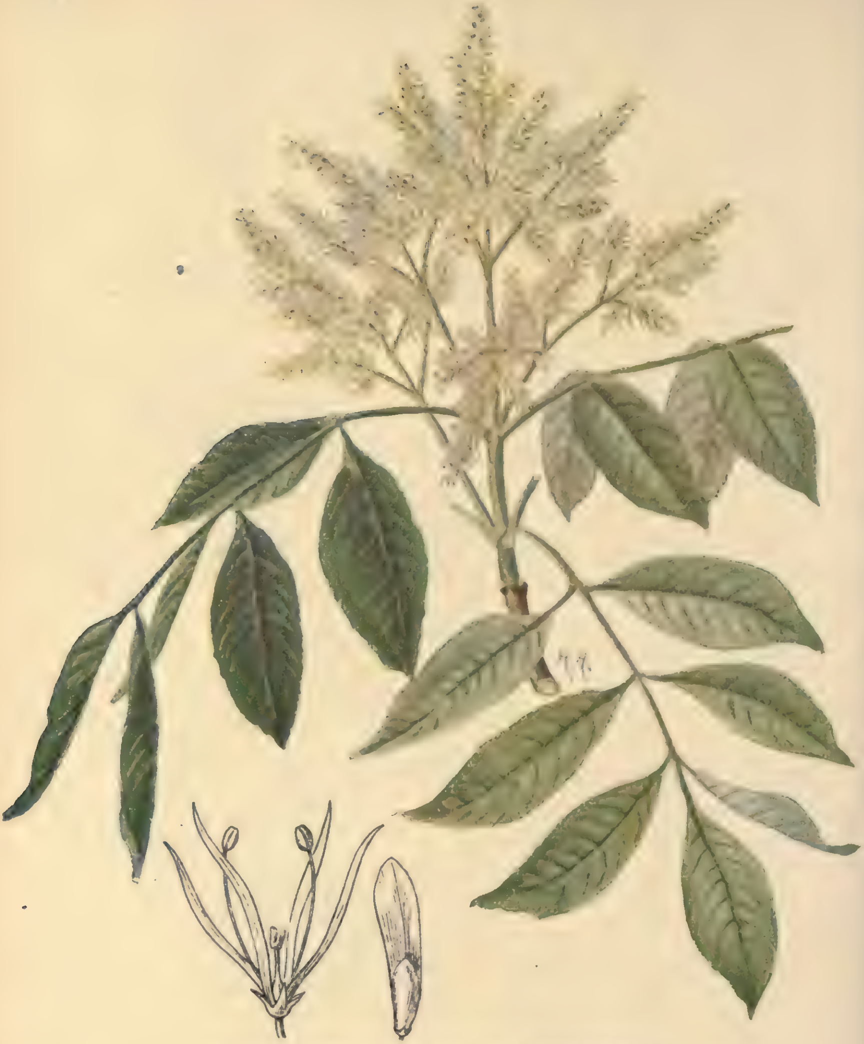


FIG. 716.—*Fraxinus ornus* (½ nat. size). Flower and fruit.

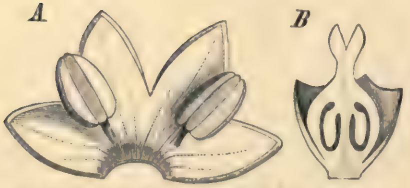


FIG. 717.—*Olea europea.* *A*, Corolla spread out. *B*, Calyx and ovary in longitudinal section. (Enlarged. After ENGLER-PRANTL.)

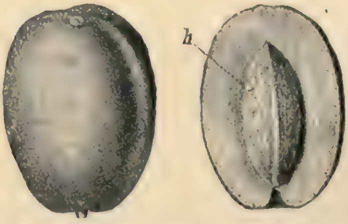


FIG. 718.—*Olea europaea.* Drupe. *h*, Stone.

This genus affords one of the best examples of seasonal dimorphism, *i.e.* the splitting of a species into two closely related forms which develop at different seasons. Since the height of the vegetative period of the Alpine meadows coincides with their annual mowing, this expresses itself in the distinction of an early form, fruiting before the meadows are cut, and a late form developing after this has taken place. *Erythraea*, Centaury (Fig. 722), anthers spirally twisted. *Menyanthes*, Bog-Bean, with alternate, trifoliolate leaves and long-stalked racemes of white flowers with hairy petals. *Limnanthemum*, aquatic plants with floating leaves.

OFFICIAL.—*Gentiana lutea* and other species yield GENTIANAE RADIX. CHIRATA is obtained from *Swertia chirata* (N. India).

Family 4. **Apocynaceae.**—Evergreen herbs, shrubs or trees, without stipules. Especially numerous in the tropics. Laticiferous cells in all parts of the plant. K5, C(5), A5, G(2). Petals contorted in the bud. Stigma ring-shaped. Carpels only united in the region of the style, free below (Fig. 723) and separating after fertilisation. Usually two follicles. Seeds provided with a tuft of hairs.

IMPORTANT GENERA.—The only British species is *Vinca minor*, the evergreen Periwinkle, occurring in woods (Fig. 726). *Nerium oleander* (Fig. 725), a native of S. Europe, is commonly cultivated. It has greyish-green, lanceolate leaves which are decussate or in whorls of three; flowers rose-coloured, sweet-scented and conspicuous. The whole plant is extremely poisonous.

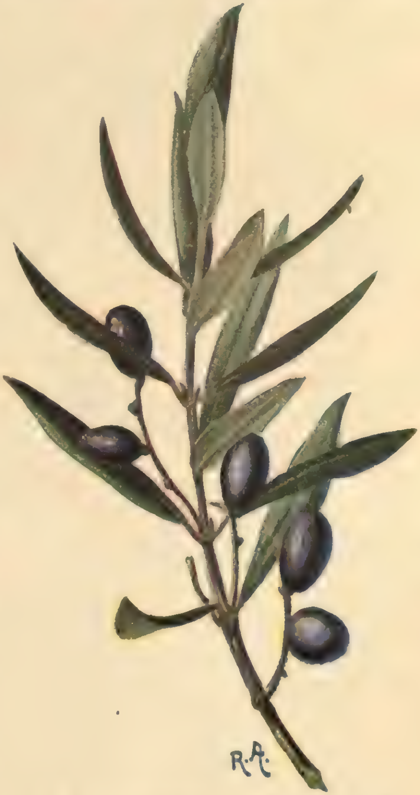


FIG. 719.—*Olea europea* in fruit. (½ nat. size.)

OFFICIAL.—*Strophanthus kombe* and *S. hispidus* (44a) (Fig. 724), lianes of tropical Africa, yield STROPHANTHI SEMINA.

Caoutchouc (45) is obtained from *Kickxia elastica* and other species, trees of tropical W. Africa. It is also obtained from numerous species of *Landolphia* (*L. Kirkii*, *Heudelotii*, *comorensis*, etc.), lianes which are, or formerly were, common throughout tropical Africa. Together with species of *Carpodinus* (Angola) which yield the root-rubber, these plants supply the main part of the rubber obtained from Africa. *Hancornia speciosa*, a tree of the dry Brazilian Campos to the south of the Amazon region, yields the "mangabeira" rubber. *Willoughbeia firma*, *W. flavescens*, and other species of this Malayan genus of lianes are also rubber-yielding plants. Gutta-percha is present in the latex of *Tabernaemontana Donnell Smithii*, which is used as a shade-tree on coffee plantations in Central America.

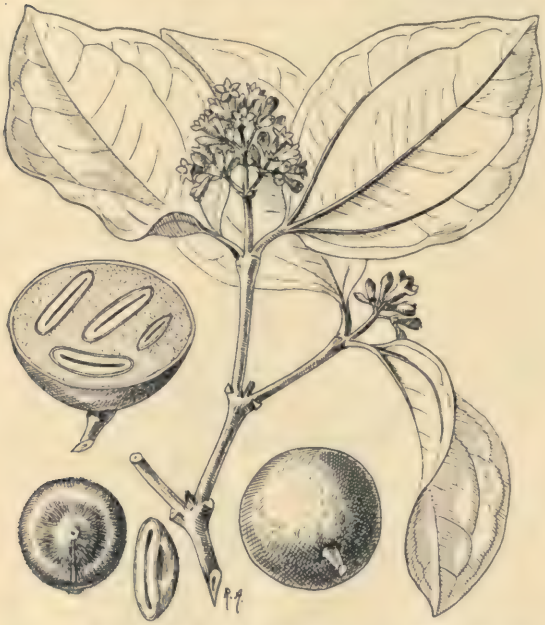


FIG. 720.—*Strychnos nux vomica* (½ nat. size). Fruit and seed whole and in cross section. *OFFICIAL* and *POISONOUS*.

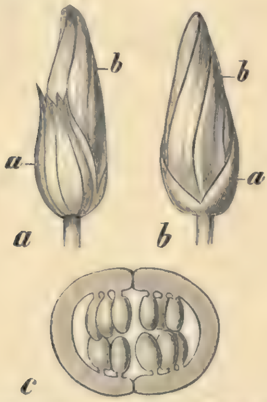


FIG. 721.—*Gentiana lutea*. *a* and *b*, Flower-buds (nat. size), showing calyx (*a*) and twisted corolla (*b*); *c*, transverse section of ovary. *OFFICIAL*. (After BERG and SCHMIDT.)

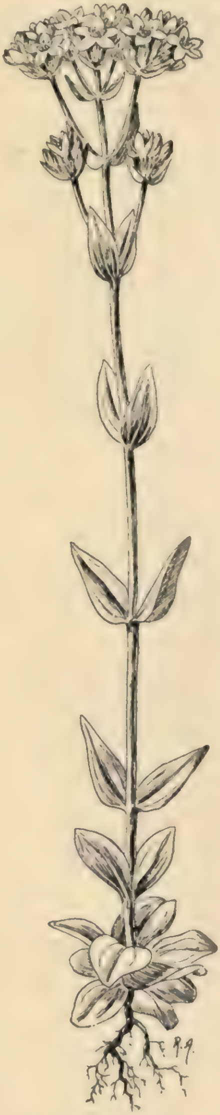


FIG. 722.—*Erythraea centaurium*. (½ nat. size.)

Since, hitherto, only some Sapotaceous plants, which are difficult to cultivate, have yielded gutta, this plant will soon take an important place in the supply.

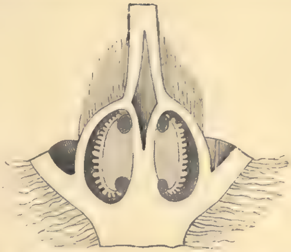


FIG. 723.—*Strophanthus hispidus.* Ovary in longitudinal section. ($\frac{10}{1}$; after ENGLER-PRANTL.)

Family 5. **Asclepiadaceae.**—Similar and closely related to the Apocynaceae. Corolla contorted in the bud; carpels free, only united by the prismatic stigma; latex in all the organs. Stamens united at the base with dorsal, nectar-secreting appendages forming a corona. The pollen

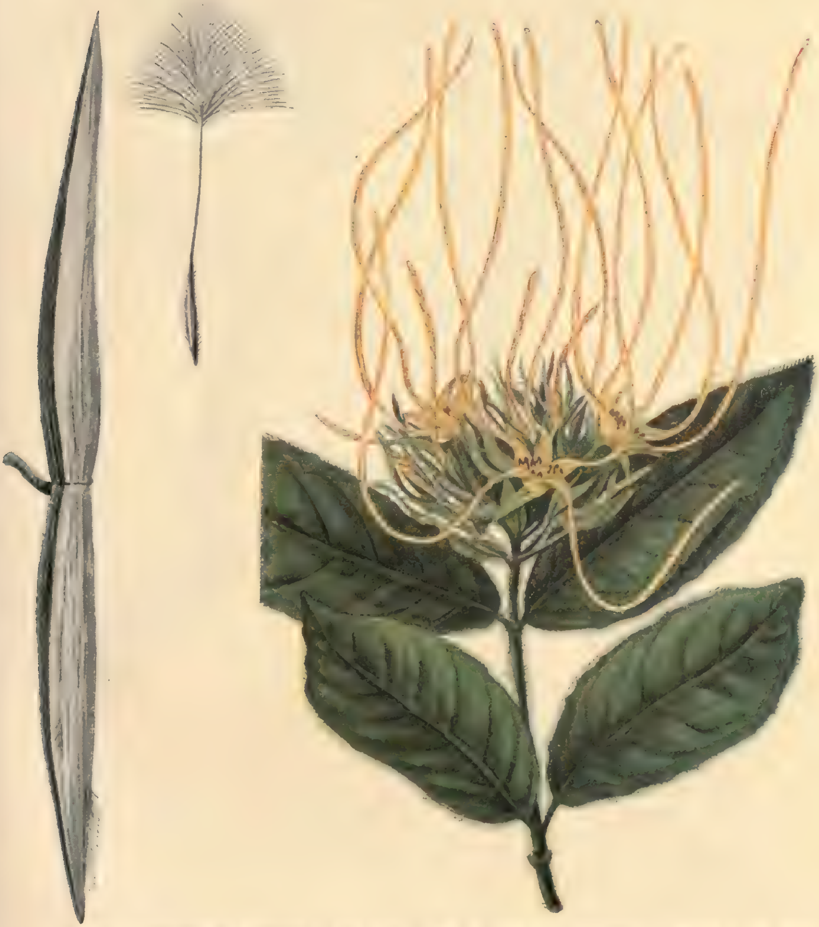


FIG. 724.—*Strophanthus hispidus* ($\frac{1}{2}$ nat. size. After MEYER and SCHUMANN). Fruit ($\frac{1}{4}$ nat. size). Seed ($\frac{1}{3}$ nat. size). (After SCHUMANN in ENGLER-PRANTL.) *OFFICIAL.*

of each pollen-sac is united into a pollinium, the stalk of which is attached to a glandular swelling (adhesive disc) of the angular stigma.

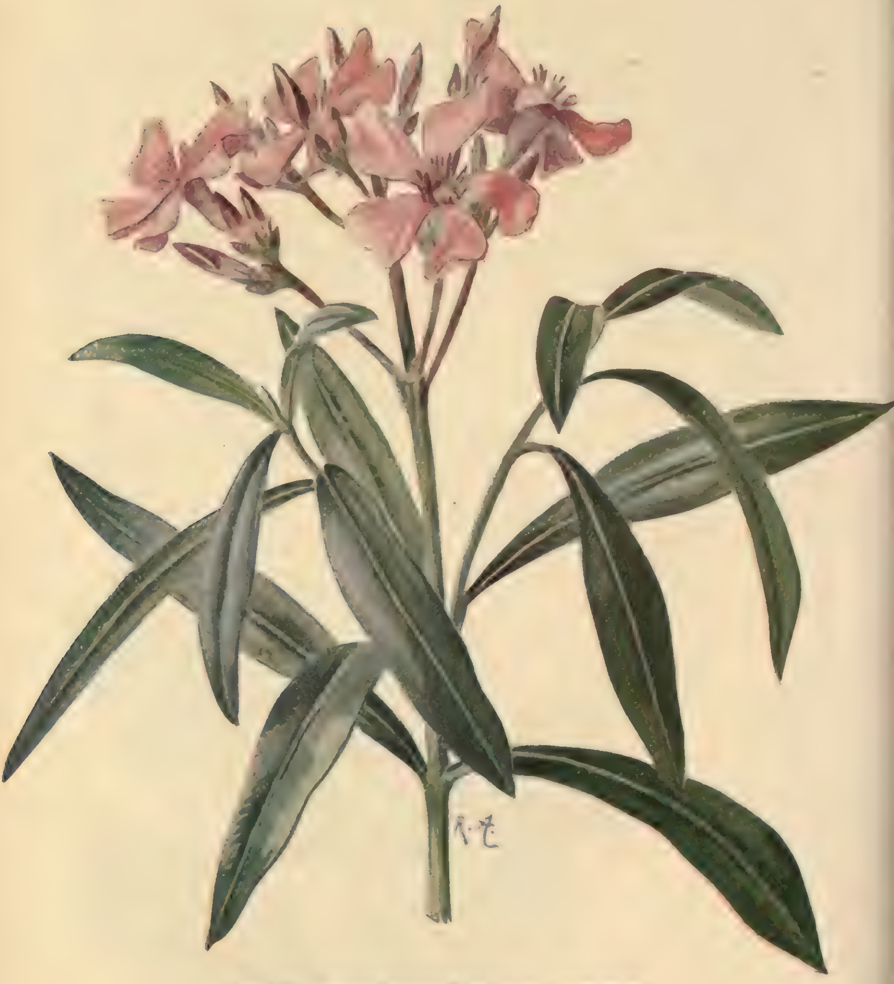


FIG. 725.—*Nerium oleander* (½ nat. size). *POISONOUS.*

These adhesive discs alternate with the stamens so that the two pollinia attached to each disc belong to the halves of two adjoining stamens. Visiting insects remove, as in the Orchidaceae, the pollinia and carry them to another flower (Fig. 727).

IMPORTANT GENERA.—*Vincetoxicum officinale* (Fig. 728) is a European herb

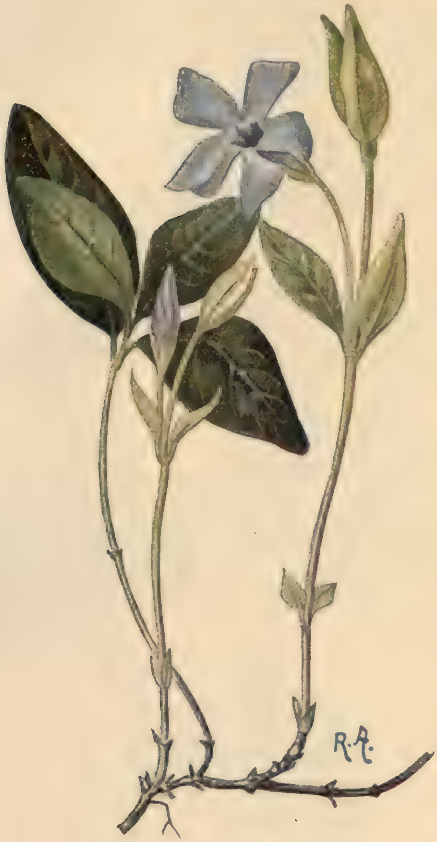


FIG. 726.—*Vinca minor* (⅔ nat. size).

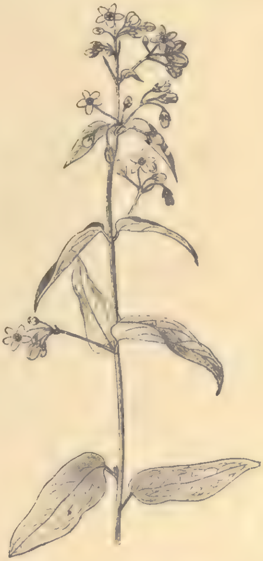


FIG. 728.—*Vincetoxicum officinale* (½ nat. size). POISONOUS.

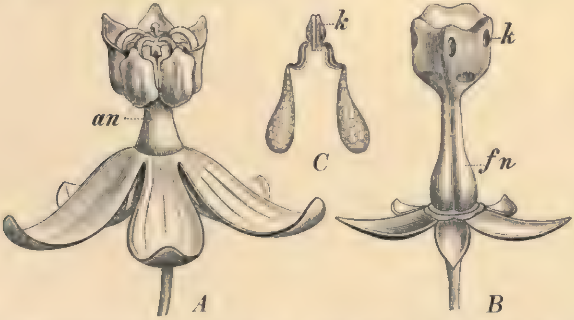


FIG. 727.—*Asclepias curassavica.* *A*, Flower; *an*, androecium (× 4); *B*, calyx and gynaeceum; *fn*, ovary; *k*, corpuscula (× 6); *C*, pollinia (more highly magnified). (After BAILLON.)

with inconspicuous, white flowers and hairy seeds which are borne in follicles; poisonous. Other forms are mostly tropical or sub-tropical. The succulent species of *Stapelia*, *Hoodia*, *Trichocaulon*, etc., which resemble Cactaceae in habit, and inhabit S. African deserts, and *Dischidia rafflesiana* (^{46}), the peculiar pitcher plant of the Malayan region, deserve special mention. *Hoya carnosa* is frequently cultivated.

Official.—*Hemidesmus indicus* yields HEMIDESMI RADIX.

Order 5. Tubiflorae

Flowers pentamerous, actinomorphic or zygomorphic. Carpels 2. Ovary superior, bilocular, with two ovules, which are frequently separated by a false septum, in each loculus.

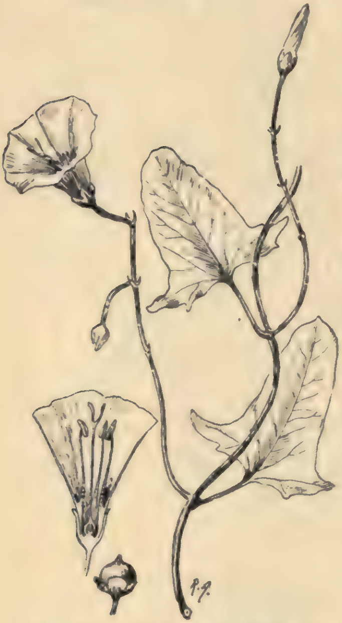


Fig. 729.—*Convolvulus arvensis* (½ nat. size). Longitudinal section of the flower and a capsule (enlarged).

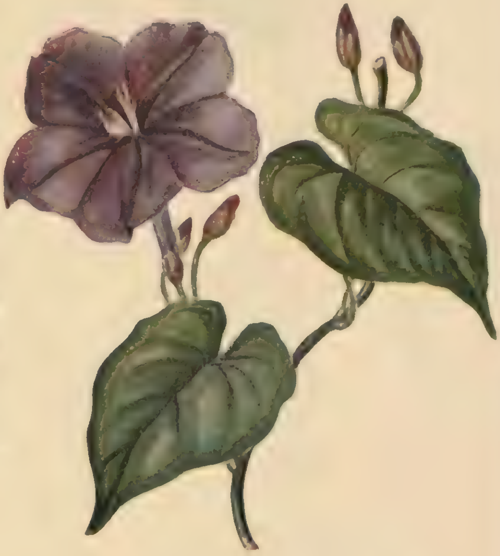


Fig. 730.—*Exogonium purga* (½ nat. size. After Berg and Schmidt). *OFFICIAL.*

Family 1. **Convolvulaceae.**—Herbs or shrubs, less commonly trees, with alternate, sagittate or cordate leaves. The majority are twining plants. Many contain latex. Corolla widely funnel-shaped, only slightly lobed; in the bud it is longitudinally folded and twisted to the right. Stamens five. Ovules basal in the two or four cavities of the ovary. Fruit, a capsule.

Important Genera.—*Convolvulus arvensis* (Fig. 729), a perennial, twining, herbaceous plant occurring everywhere by waysides, and as a weed in corn-fields.

Flowers solitary, long-stalked, situated in the axils of the leaves and sometimes in the axils of the bracteoles of another flower. *Calystegia* has two large bracteoles placed immediately beneath the calyx. *C. sepium.* The Dodder (*Cuscuta*) (47) is a slender parasitic plant containing very little chlorophyll, which attaches itself by means of haustoria to a number of different host plants. The small flowers are borne in dense clusters (cf. p. 229, Fig. 202). *Ipomoea* is for the most part a tropical genus; several species are cultivated as ornamental plants. *I. pescaprae* is one of the strand plants of tropical countries.

OFFICIAL.—JALAPA is obtained from *Exogonium purga* (Fig. 730), a twining plant, with tuberous lateral roots, occurring on the wooded, eastern slopes of the Mexican table-land. SCAMMONIAE RADIX is the dried root of *Convolvulus Scammonia* (Asia Minor).

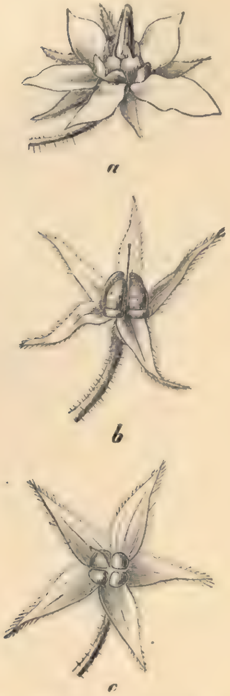


FIG. 731.—*Borago officinalis.* *a*, Flower; *b* and *c*, fruit (nat. size).

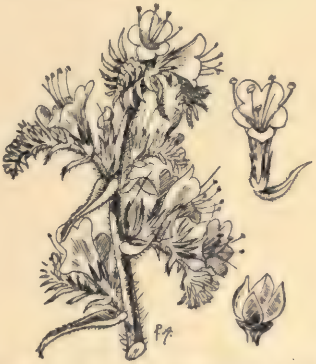


FIG. 732.—*Echium vulgare.* Inflorescence (½ nat. size). Single flower and fruit, composed of four nutlets (enlarged).

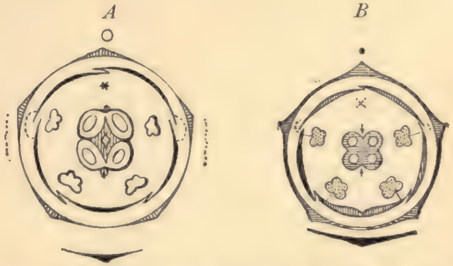


FIG. 733.—Floral diagrams of *Verbena officinalis* (*A*), (after EICHLER), and of *Lamium* (Labiatae) *B*.

Family 2. **Polemoniaceae.**—Carpels usually three. No milky juice. *Polemonium coeruleum* occurs in Britain. *Cobaea scandens* and *Phlox* are cultivated.

Family 3. **Hydrophyllaceae.** — K 5, C (5), A 5, G $\underline{(2)}$. Inflorescence a cincinnus.

Family 4. **Boraginaceae.**—Herbs with alternate leaves. These and the stems are covered with coarse hairs (Asperifoliaceae). Inflorescence always cincinnal (48). Flowers actinomorphic or zygomorphic. Petals frequently provided with scales

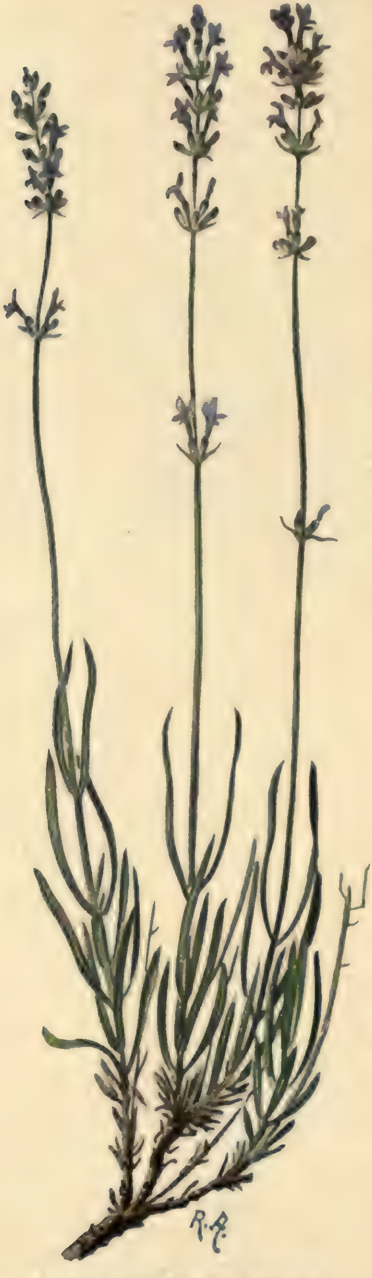


Fig. 735.—*Lavandula vera* (½ nat. size). *Official.*

standing in the throat of the corolla. Ovary always bilocular but divided by false septa into four one-seeded nutlets. The style springs from the midst of the four-lobed ovary. Ovules pendulous. Fruit, a schizocarp, separating into four portions (Figs. 731, 732).

Genera. — *Symphytum* (Comfrey), *Borago* (Borage), *Anchusa* (Alkanet), *Echium* (Bugloss), *Myosotis* (Forget-me-not), are among the commonest and most conspicuous herbaceous plants of our flora; all have entire, alternate leaves, covered with harsh hairs and relatively large flowers of a lighter or darker blue, grouped in complicated inflorescences. In *Pulmonaria officinalis*, which flowers in spring, the colour of the corolla changes from red to a bluish violet. *Cerinthe* is completely glabrous, and has a waxy covering to the epidermis. *Heliotropium*, a favourite ornamental plant, has an undivided ovary.

Family 5. **Verbenaceae.**—Shrubs or trees, rarely herbs, with zygomorphic flowers. K 5, C (5), A 4, G (2). Distin-

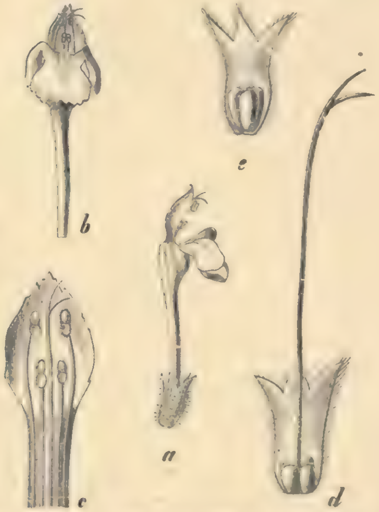


Fig. 734. *Galeopsis ochroleuca.* *a*, Flower; *b*, the same with calyx removed; *c*, corolla cut open, showing stamens and style; *d*, calyx and gynaeceum; *e*, fruit. *Official.* (*a*, *b*, nat. size; *c*, *d*, *e* × 2.)

guished from the following family by the terminal position of the style (Fig. 733 *A*). Only *Verbena officinalis* occurs in Britain. *Lantana* is a widely spread weed in the tropics. *Tectona grandis* (49), a deciduous tree of the dry regions of the East Indies, yields the important timber TEAK. *Avicennia* (50), trees of the mangrove vegetation, with viviparous fruits and pneumatophores (Fig. 213). *Clerodendron* (51) includes some myrmecophilous species.

Family 6. **Labiatae.**—Herbs or shrubs with quadrangular stems and decussate leaves without stipules. Leaves simple; plants often aromatic owing to the presence of glandular hairs. Flowers solitary in the axils of the leaves, or forming apparent whorls. The small inflorescences are dichasia or double cincinni, and are often united in larger, spike- or capitulum-like inflorescences. Flower zygomorphic (Fig. 734). Calyx, gamosepalous, with five teeth; corolla two-lipped, the upper lip consisting of two, the lower of three petals; stamens in two pairs, two long and two short, rarely only two. Ovary of two carpels, each of which is deeply indented in the plane of the false septum. Style springing from between the lobes; stigma bifid. A ring-shaped nectary situated at the base of the ovary. Fruit, a schizocarp, consisting of four nutlets.

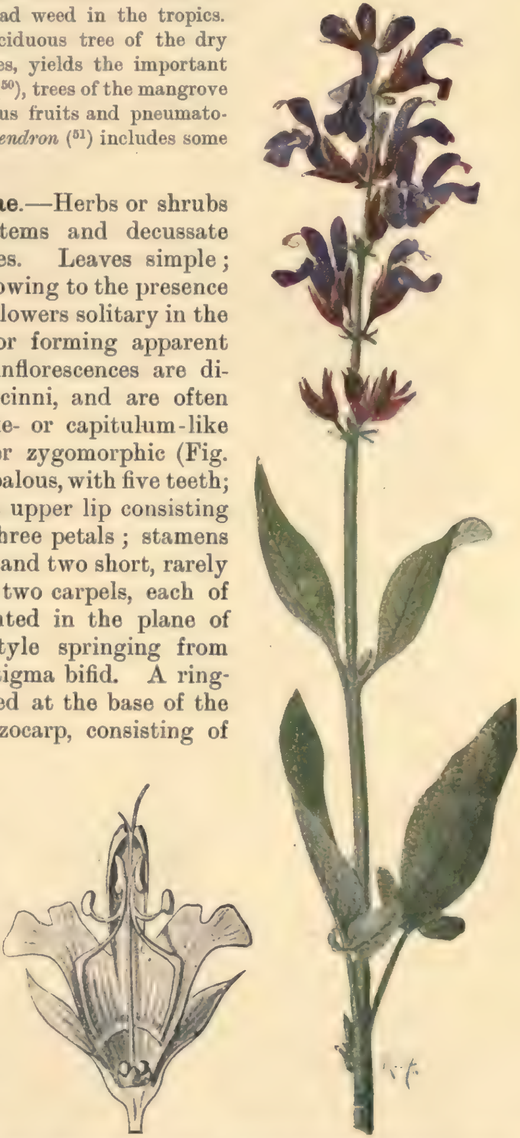


FIG. 736.—*Salvia officinalis.* Flowering shoot (½ nat. size). Tubular corolla slit open to display the stamens (enlarged).

IMPORTANT GENERA.—The Labiatae include a considerable proportion of our commonest native spring and summer flowers; *Lamium*, *Galeopsis*, and *Stachys* have the upper lip helmet-shaped, *Ajuga* has it very short, while in *Teucrium* the upper lip is deeply divided. *Nepeta* and *Glechoma* differ from the majority of the order, in having the posterior stamens longer than those of the anterior pair. *Salvia*, Sage (52), is a genus containing numerous species; the flowers are protandrous and are characterised by the suppression of two of the stamens usually present (Fig. 736). The two fertile stamens have a very long connective, with the anterior theca, in which pollen is formed, protected beneath the upper lip. The posterior theca, the development of which differs in the species, projects into the entrance of the corolla tube leading to the nectary (cf. p. 312, Fig. 244). A bee visiting the flower, presses this theca upwards and thus brings down the other arm of the lever, formed by the elongated connective, upon its back. In older flowers the bifid stigma occupies such a position that it will rub off pollen brought by an insect from another flower. Many species of *Salvia* are cultivated as ornamental plants, and are often conspicuous, rather by reason of their brightly coloured bracts than by their flowers. Labiatae are especially abundant in the xerophytic formation of shrubby plants in the Mediterranean region to which the name Maquis is given: *Salvia officinalis*, *Marrubium*, *Phlomis*, and species of *Lavandula*. *Rosmarinus officinalis* is a showy shrub with small narrow leaves revolute at the margin, and bright blue flowers with only two fertile stamens. Many species are grown as kitchen herbs, *e.g.* *Origanum majorana*, *Satureja hortensis*, *Ocimum basilicum*, *Salvia* and *Thymus*. *Thymus vulgaris* from the Mediterranean, like our native *T. serpyllum*, is a low, shrubby plant with polygamous flowers; there are larger, hermaphrodite and small, purely female flowers. Some species of *Mentha* are similar. The widely cultivated *M. piperita* is a hybrid between *M. viridis* and *M. aquatica*; it is completely sterile, and has been propagated by runners from ancient times. *M. crispa*, another commonly cultivated form, is a crispate variety of *M. viridis*; *M. longifolia*, var. *undulata*, *M. sylvestris*, etc.

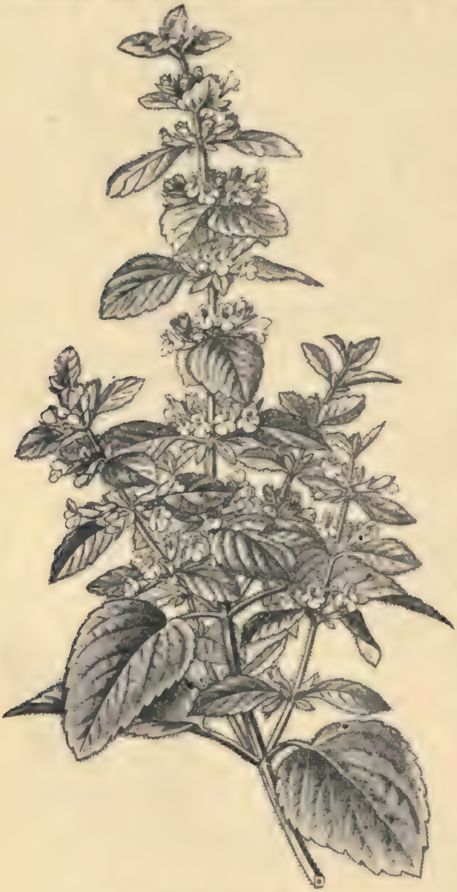


FIG. 737.—*Melissa officinalis* (½ nat. size. After BERG and SCHMIDT).

OFFICIAL.—*Rosmarinus officinalis* yields OLEUM ROSMARINI. *Lavandula vera* (Mediterranean region), OLEUM LAVANDULAE. *Mentha piperita*, OLEUM MENTHAE PIPERITAE. *M. viridis*, OLEUM MENTHAE VIRIDIS. *M. arvensis* and *M. piperita* yield MENTHOL. *Thymus vulgaris* and *Monarda punctata* yield THYMOL.

Order 6. Personatae

The Personatae are connected by the small family Nolanaceae to the Convolvulaceae, from which the Tubiflorae are also derived. The flowers are actinomorphic or zygomorphic. Their typical form has also the floral formula K5, C(5), A5, G$(\underline{2})$. There are, however, no false septa in the ovary and the number of ovules is usually a larger one.

Family 1. **Solanaceae.**—Herbs or small woody plants, with alternate, exstipulate leaves, and nearly always actinomorphic flowers, K5, C(5), A5, G$(\underline{2})$. Corolla expanded or tubular; petals plaited in the bud. Ovary bilocular, septum inclined obliquely to the median plane. Ovules numerous, on a thick placenta. Fruit, a capsule or a berry. Seeds with endosperm; embryo usually curved (Fig. 738). In many Solanaceae, as will be further referred to in the special descriptions below, the inflorescences exhibit apparent, extra-axillary branches and paired leaves. Anatomically the order is characterised by possessing bicollateral vascular bundles.

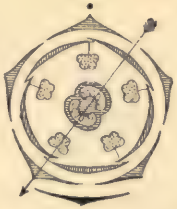


FIG. 738.—Solanaceae. Floral diagram (*Petunia*).

IMPORTANT GENERA AND SPECIES.—(*a*) Fruit, a berry: The Deadly Nightshade (*Atropa Belladonna*, Fig. 739) is a perennial herb of shrubby habit, springing from an underground rhizome. It is a native of Europe and western Asia, occurring in less dense woods. The shoots are, to begin with, orthotropous and radial, and bear alternate leaves and a terminal flower, which only rarely produces fruit. Below this terminal flower branching and the development of leaves commences in, as a rule, three, equally vigorous, lateral shoots. Each lateral branch with its further cincinnal branching forks and assumes a dorsiventral habit. By the predominance of one of the two axillary shoots and the carrying up of the subtending bract upon it, the terminal flower at each grade of branching becomes apparently axillary. The large, subtending bract is borne up beside the smaller one belonging to the next higher axillary bud, which is usually undeveloped, so that the leaves appear to be borne in pairs. Flower with a short, wide, tubular corolla of a dirty purple colour. Calyx enlarging after fertilisation beneath the bluish-black fruit; the position of the obliquely placed septum of the latter is recognisable externally by the presence of a shallow groove.

Many species of *Solanum* occur as weeds. Flowers actinomorphic. *S. nigrum*, Nightshade; *S. dulcamara*, Bitter-sweet (Fig. 740), is a shrubby plant, climbing by means of its stems and petioles, and especially common in thickets by the banks of streams and similar situations. *S. tuberosum*, the Potato. *Lycopersicum*, the Tomato. *Capsicum annuum*, Spanish Pepper, has a dry, berry-like fruit. These plants resemble *Atropa* in their branching and the position of their leaves.

(*b*) Fruit a capsule: *Datura Stramonium*, Thorn-apple (Fig. 741), is an annual plant, widely spread in Europe, Asia, and N. America. It has incised, palmately-veined leaves and large, white, terminal flowers. The spiny fruits split at the summit into four valves. The first terminal flower is developed early, and the plant then exhibits profuse dichasial branching. Since the subtending leaves are adherent to the axillary shoots, which as a rule develop equally, the branching appears to be extra-axillary, a terminal flower or fruit being situated in the fork.

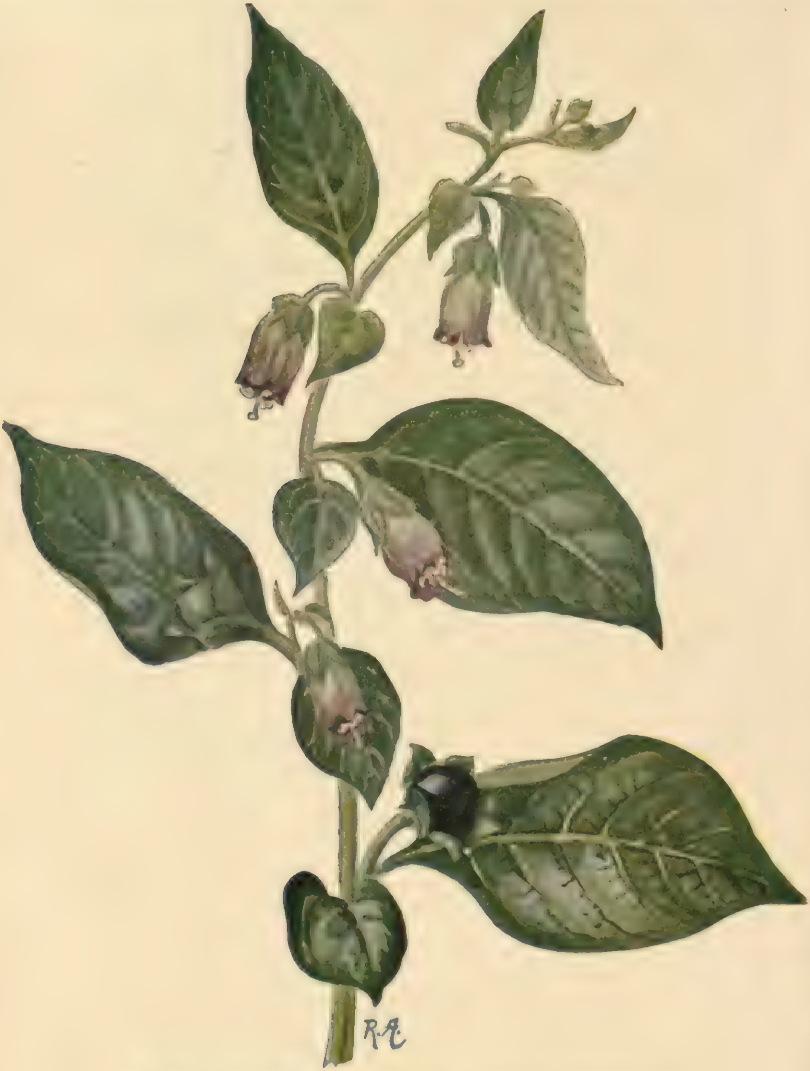


FIG. 739.—*Atropa Belladonna* ($\frac{1}{2}$ nat. size). *OFFICIAL* and *POISONOUS.*

Nicotiana tabacum (Figs. 742, 743) is a South American plant with numerous cultivated varieties, which are grown both in Europe and the tropics. Its large alternate leaves, which bear numerous glandular hairs, form, after being dried and prepared, TOBACCO. Flowers elongated and tubular, borne in terminal panicles. *Hyoscyamus niger*, the Henbane (Fig. 744), is an annual plant occurring in Central Europe, North Africa, and Western Asia. The radical leaves have long stalks, those of the flowering stem are sessile ; they are all clothed with glandular hairs. Flowers slightly zygomorphic, of a dull yellowish-violet colour with darker markings ; inflorescence, a cincinnus. Fruit, a pyxidium. *Petunia* and *Salpiglossis* are favourite garden plants with obliquely zygomorphic flowers.

All Solanaceae are more or less poisonous partly on account of the presence of considerable amounts of alkaloids or poisonous glucosides. Species of *Solanum*, *Atropa*, *Datura*, *Hyoscyamus*, and *Nicotiana* are among the most poisonous plants met with in this country.

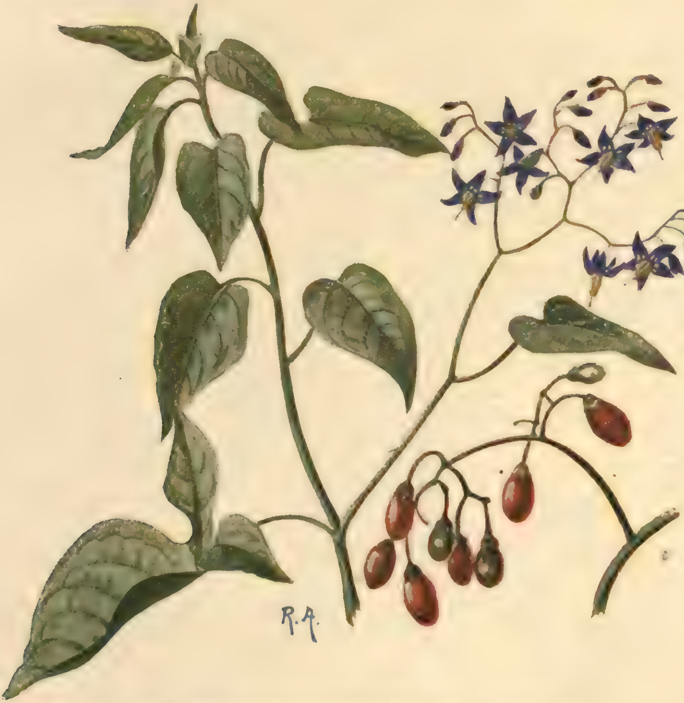


FIG. 740.—*Solanum dulcamara* (½ nat. size). *POISONOUS.*

OFFICIAL.—*Capsicum minimum* yields CAPSICI FRUCTUS, *Atropa belladonna* yields BELLADONNAE FOLIA, BELLADONNAE RADIX and ATROPINA. *Datura Stramonium*, STRAMONII SEMINA and STRAMONII FOLIA. *Hyoscyamus niger*, HYOSCYAMI FOLIA.

Family 2. **Scrophulariaceae.**—Herbs, with opposite or alternate, exstipulate leaves. Flowers zygomorphic. Corolla not plaited in the bud. Number of stamens often incomplete. Carpels median (Fig. 745). Fruit, a bilocular capsule.

IMPORTANT SUB-FAMILIES AND GENERA.—(*a*) *Antirrhineae*, not parasitic.

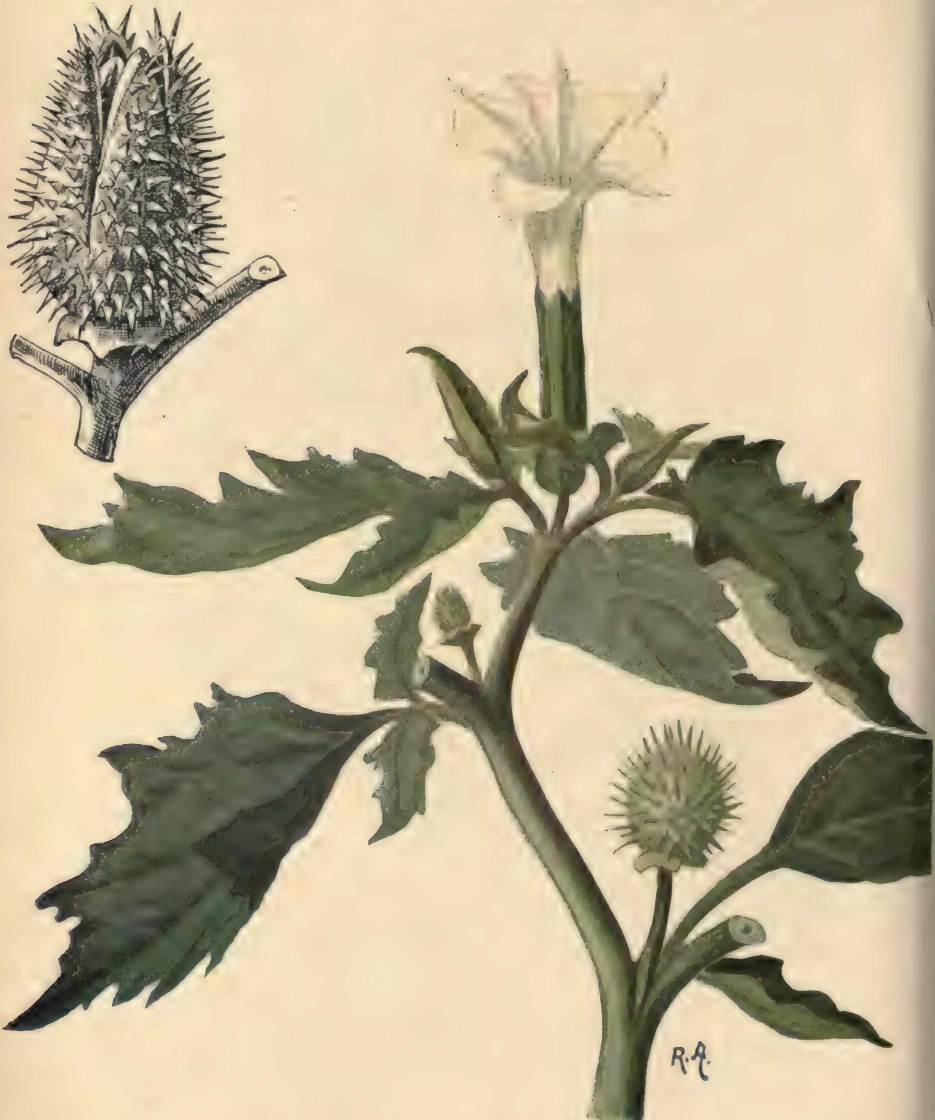


FIG. 741.—*Datura Stramonium* (½ nat. size). Mature fruit after dehiscence. OFFICIAL and POISONOUS.

Verbascum (Fig. 746), the Mullein; biennial herbs, which in the first season form a large rosette of leaves from which the erect inflorescence arises in the second year. The inflorescence sometimes bears sessile dichasia of 2-3 flowers in a terminal spike; in other cases by the development of branches from the lower leaf-axils it becomes a branched panicle. The single flowers have five stamens, and are only slightly zygomorphic; the three posterior stamens have hairy filaments, and are further distinguished from the two anterior stamens by the transverse position of their anthers. *Digitalis*, Foxglove (Figs. 747, 748), has an obliquely campanulate corolla and four stamens. The flowers hang from one side of the obliquely ascending raceme. *Scrophularia* has a two-lipped corolla with a very short lower lip. The corolla in *Linaria* and *Antirrhinum* is spurred. *Veronica* and *Gratiola* have only two fertile stamens.

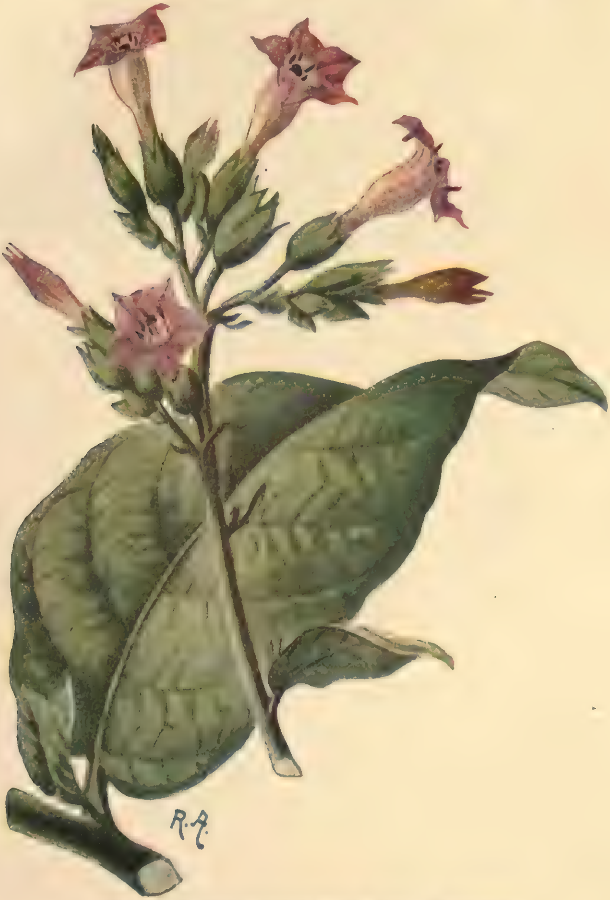


FIG. 742.—*Nicotiana tabacum* (½ nat. size). *POISONOUS.*

(*b*) *Rhinantheae.*—This group includes a number of closely related genera which have adopted a more or less completely parasitic mode of life. The most completely parasitic form is *Lathraea* (cf. p. 211), the species of which have no trace of chlorophyll ; *L. squamaria*, the Toothwort, is parasitic on the roots of the Hazel. Many (*e.g. Tozzia, Bartsia, Euphrasia, Odontites, Pedicularis, Melampyrum, Alectorolophus*) are semiparasitic. Although they possess green leaves they attach themselves by means of haustoria to the roots of other plants, from which they obtain nutrient materials. Further details regarding the mode of life and development of these forms, and the seasonal dimorphism they exhibit, will be found in the literature cited (53).

OFFICIAL.—*Digitalis purpurea* yields DIGITALIS FOLIA.

Family 3. **Orobanchaceae.**—Root-parasites, without chlorophyll. Flower as in the Scrophulariaceae, but with a unilocular ovary. Several British species of *Orobanche*, parasitic on various host plants (Fig. 749).

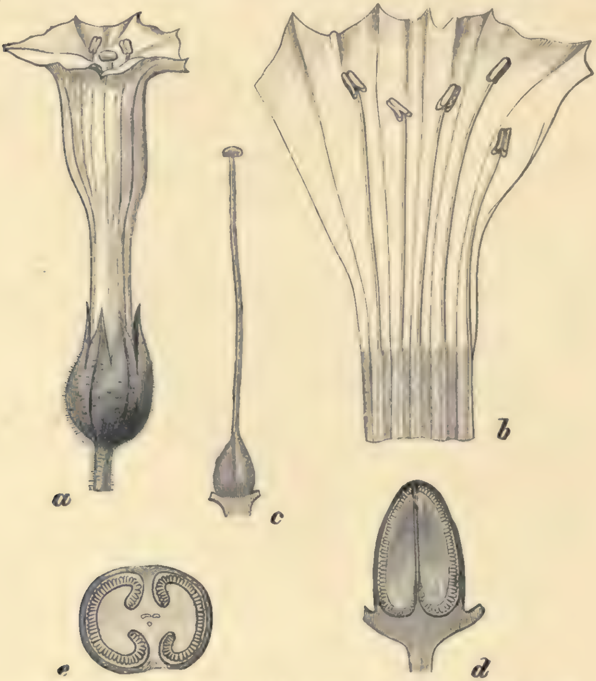


FIG. 743.—*Nicotiana tabacum.* *a*, Flower ; *b*, corolla, cut open and spread out flat ; *c*, ovary ; *d* and *e*, young fruit. (*a*, *d*, *c*, nat. size ; *e*, *d*, × 2.)

Family 4. **Bignoniaceae.**—Woody plants, in many cases climbers. Stamens 4, corolla two-lipped. Seeds winged. *Catalpa bignonioides, Tecoma radicans*, ornamental plants from N. America.

Family 5. **Gesneriaceae.**—Tropical herbs with a unilocular ovary which is sometimes superior, in other cases inferior, and 4 or 2 stamens. Frequently cultivated on account of the beautiful colour of their flowers, *e.g. Gloxinia, Aeschynanthus, Achimenes. Ramondia pyrenaica* is one of the few European representatives. *Streptocarpus* (54) *polyanthus* only develops one of its cotyledons, which persists and attains a large size ; the inflorescences arise at the base of the cotyledon.

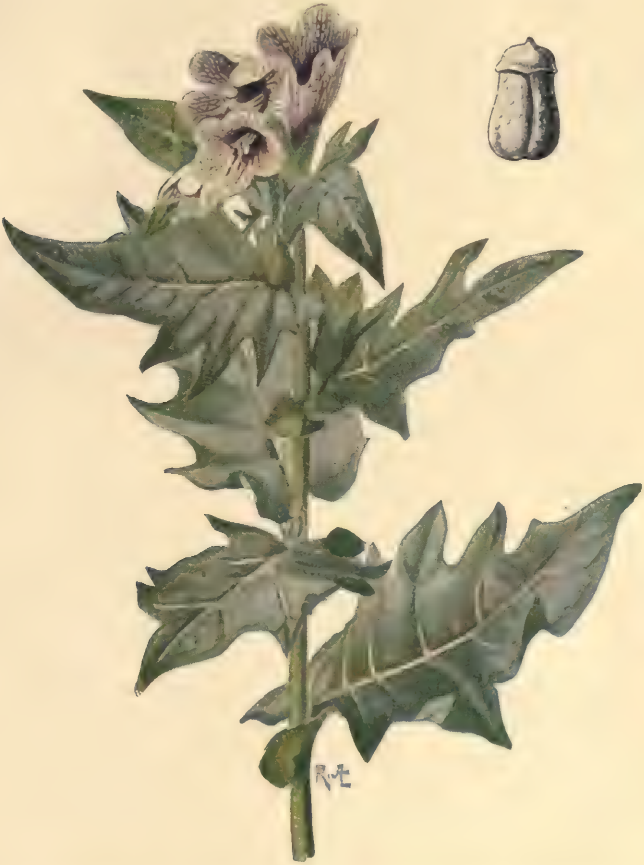


Fig. 744.—*Hyoscyamus niger*. Flowering shoot and fruit (½ nat. size). *Official* and *Poisonous*.

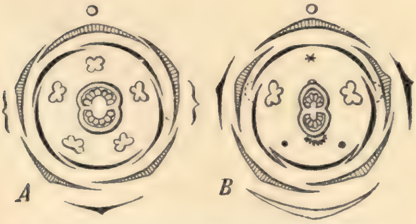


Fig. 745.—Scrophulariaceae. Floral diagrams. *A*, *Verbascum* ; *B*, *Gratiola*. (After Eichler.)

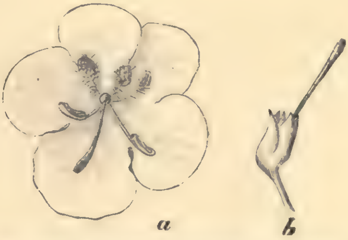


Fig. 746.—*Verbascum thapsiforme*. *a*, Flower ; *b*, calyx and style (nat. size).

Family 6. **Lentibulariaceae.**—Marsh- or water-plants with a spurred corolla and only two (anterior) stamens. They capture and digest insects. *Utricularia* (55), aquatic plants provided with bladder-like traps; in the tropics also terrestrial and epiphytic forms. *Pinguicula*, with a rosette of radical leaves, the margins of which are inrolled (cf. Fig. 47 and p. 237).

Family 7. **Acanthaceae.**—Herbs with decussately arranged leaves and quadrangular stems. The fruits are bilocular capsules and spring open when mature. Numerous species occur as undergrowth in tropical forests. Species of *Acanthus* occur in the Mediterranean region. Their large, pinnately-lobed leaves, the lobes terminating in spines, figure in Grecian art on the capitals of pillars, etc.

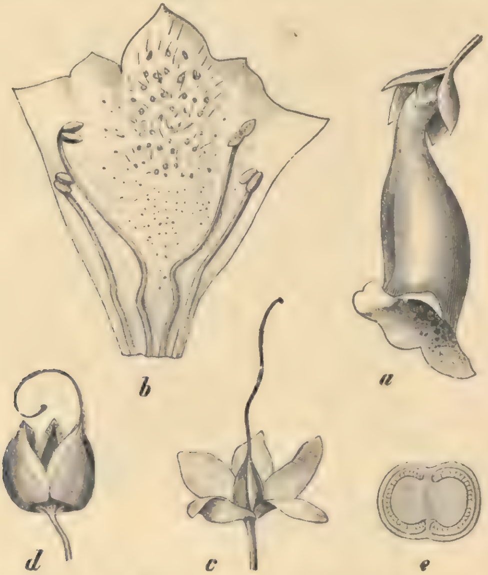


FIG. 747.—*Digitalis purpurea.* *a*, Flower; *b*, corolla cut open and spread out; *c*, calyx and pistil; *d*, fruit after dehiscence; *e*, transverse section of fruit (nat. size). *OFFICIAL.*

Family 8. **Plantaginaceae.**—Herbs with a basal rosette of leaves and long-stalked spikes of crowded flowers. Flowers tetramerous, actinomorphic. Corolla membranous. Ovary bilocular. Style long and papillate.

GENERA.—The native species of *Plantago* (56), the Plantain, are markedly protogynous (cf. Fig. 241, p. 310); the young heads or spikes show the pale-coloured stigmas projecting before the corolla has opened (Fig. 750). Transitional forms from anemophily to entomophily are found. *Litorella lacustris* is an aquatic plant with a spike of three flowers; two female flowers are situated at the base, while the male flower has a long stalk.

Order 7. Rubiinae

Plants of diverse habit with opposite leaves. In contrast to the preceding order the flowers have a sympetalous corolla associated with an inferior ovary. Flowers tetramerous or pentamerous.

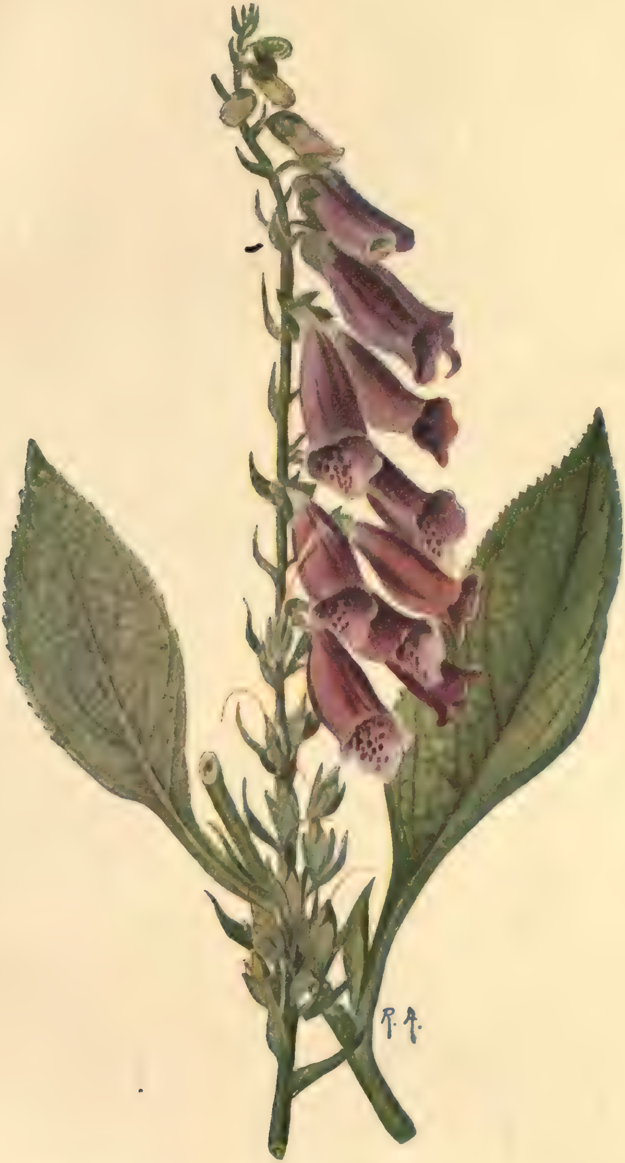


FIG. 748.—*Digitalis purpurea* (½ nat. size). *OFFICIAL* and *POISONOUS*.

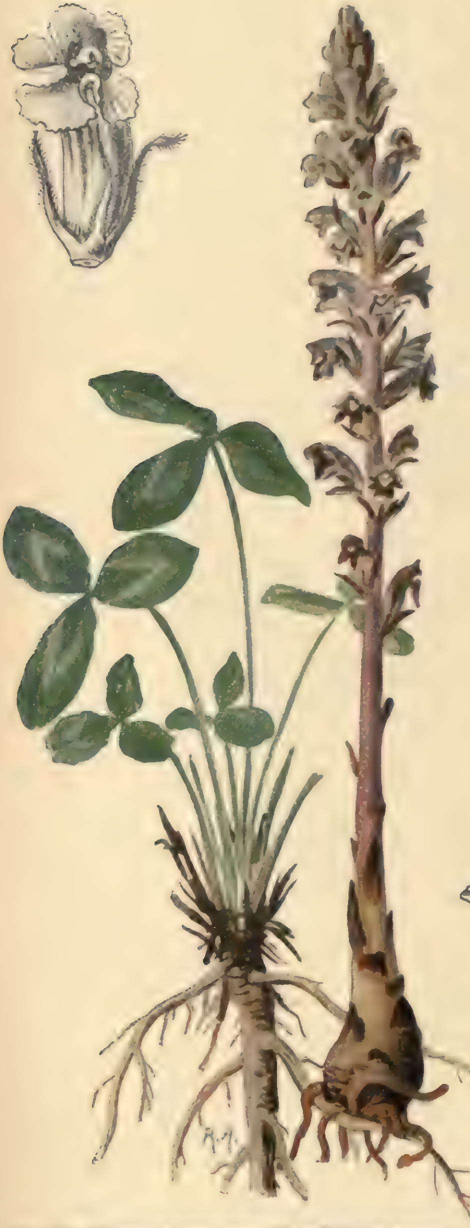


FIG. 749.—*Orobanche minor*, parasitic on *Trifolium repens* (½ nat. size). Single flower (enlarged).

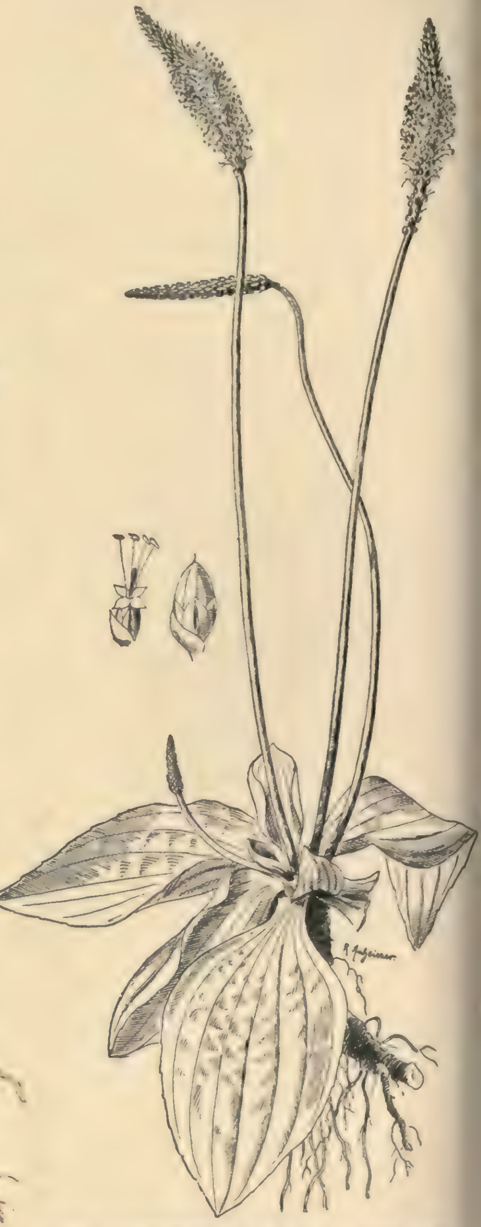


FIG. 750.—*Plantago media* (⅔ nat. size). Single flower and fruit (enlarged).

Ovary bi- or tri-locular. Stamens epipetalous. Calyx very inconspicuous.

Family 1. **Rubiaceae.**—Herbs, shrubs, or trees, with simple, decussate leaves and stipules. Flowers actinomorphic. Ovary bilocular.

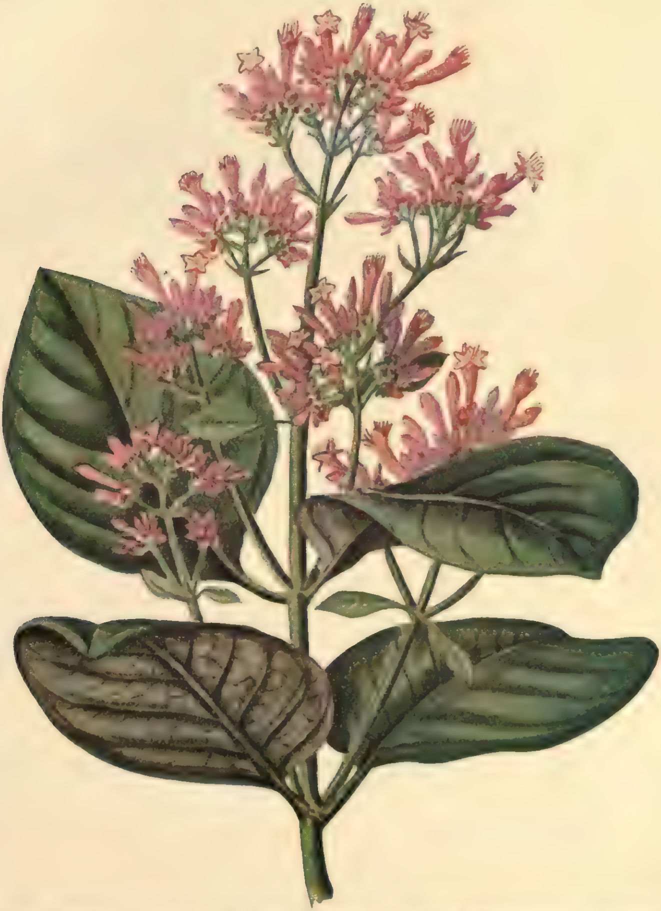


FIG. 751.—*Cinchona succirubra* (nat. size). *OFFICIAL.* (After SCHUMANN and ARTHUR MEYER.)

SUB-FAMILIES AND IMPORTANT GENERA.—(*a*) *Cinchoneae*, woody plants with scaly stipules and numerous seeds in each cavity of the ovary. *Cinchona* is a genus from the S. American Andes, now cultivated in the mountains of nearly all tropical colonies (Figs. 751, 752). Stipules deciduous. Flowers in terminal panicles; corolla tubular, with an expanded terminal portion fringed at the margin. Fruit, a septicidal capsule, the valves of which, after dehiscence has taken place, are still held together above by the small calyx. Seeds with a broad, membranous wing. *Ourouparia* (57) is a genus of climbing plants found in the Malayan Archipelago ; the hook-like organs specialised for climbing are the stalks of reduced inflorescences, which are sensitive to contact. The flowers are associated together in spherical inflorescences resembling those of the commonly grown ornamental shrub *Cephalanthus*.

(*b*) *Coffeae*.—Stipules scaly. Each loculus of the ovary with a single seed. *Coffea*, the Coffee plant, is a shrub ; *C. arabica* (Fig. 753) and *C. liberica* are important economic plants, originally derived from Africa, and now cultivated throughout the tropics. The pentamerous, snow-white flowers, which have a similar scent to that of Orange blossom, and the bright red fruits contrast with the shining, dark-green foliage, and make a coffee plantation attractive both in appearance and in scent. The pericarp becomes differentiated into a succulent exocarp and a stony endocarp. The minute embryo is embedded in the horny endosperm with which the seed is filled ; the seed-coat is very thin. The remarkable myrmecophilous plants (cf. Fig. 207, p. 237) of the Malayan Archipelago, *Myrmecodia* (58) and *Hydnophytum*, also belong to this group ; the former has spiny roots. *Uragoga Ipecacuanha*, a small herbaceous plant or undershrub, is a native of Brazil, especially of the province of Matogrosso. The stipules have an

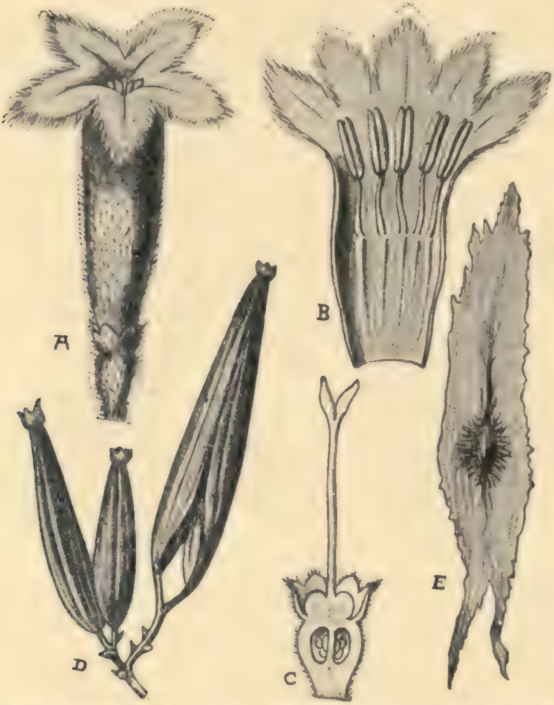


FIG. 752.—*Cinchona succirubra*. *A*, Flower. *B*, Corolla split open. *C*, Ovary in longitudinal section. *D*, Fruit. *E*, seed. (*D*, nat. size, the others enlarged.) After A. MEYER and SCHUMANN. *OFFICIAL*.

incised margin, and the inflorescence is a terminal head of flowers surrounded by a number of bracts (Fig. 754). The fruits are small berries. The plant is cultivated in suitable localities in valleys on the south side of the Himalayas.

(*c*) *Stellatae.*—This is the only subdivision of the family which is represented in Europe; *Galium*, *Rubia*, *Asperula* (Woodruff). These genera are characterised by the resemblance of the stipules to the leaves (Fig. 755); usually a whorl of six members is borne at each node, but sometimes the number is increased, and in *Rubia* it is reduced to four by the union of the stipules in pairs. The leaves are easily distinguished from the stipules by the presence of buds in their axils. Flowers usually tetramerous; a single seed in each loculus of the ovary. Fruit a schizocarp splitting into nut-like, partial fruits. Fruits often provided with hooks.

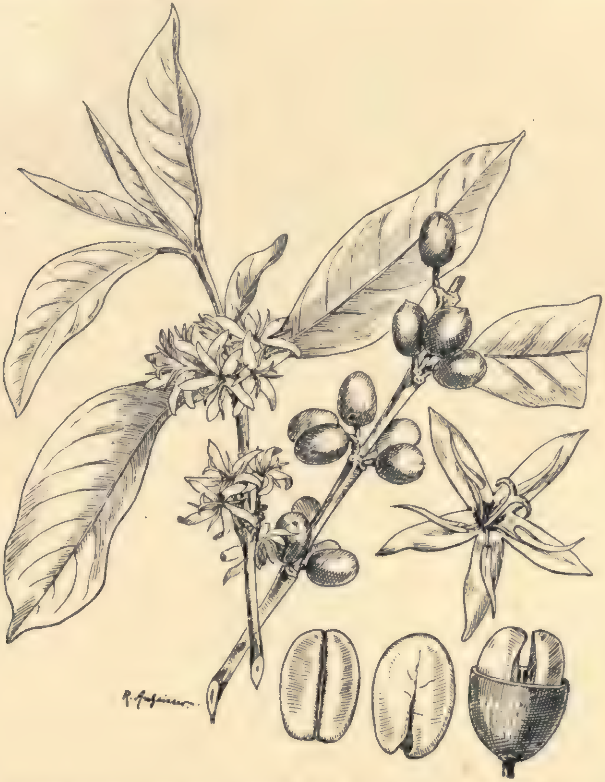


FIG. 753.—*Coffea arabica* ($\frac{1}{2}$ nat. size). Single flower, fruit, seed enclosed in endocarp, and freed from it (about nat. size).

OFFICIAL.—*Cinchona succirubra* yields CINCHONAE RUBRAE CORTEX. QUININE is obtained from this and other species of *Cinchona*. *Uragoga* (*Psychotria*) *Ipecacuanha* yields IPECACUANHA. CATECHU is obtained from *Ourouparia* (*Uncaria*) *gambir*.

Family 2. **Caprifoliaceae.**—Woody plants, usually without stipules. Flowers sometimes zygomorphic. Ovary usually trilocular. Fruit a berry or drupe.

Sub-Families and Important Genera.—(*a*) *Sambuceae*, with actinomorphic flowers and drupes. *Viburnum*, leaves simple, fruit one-seeded. *Sambucus*, Elder, with imparipinnate leaves, glandular stipules, and three stones in each fruit. *S. nigra* (Fig. 756) is a common European shrub. The flat-topped inflorescences are panicles consisting of decussately arranged main branches which ultimately bear the flowers in small cymes.

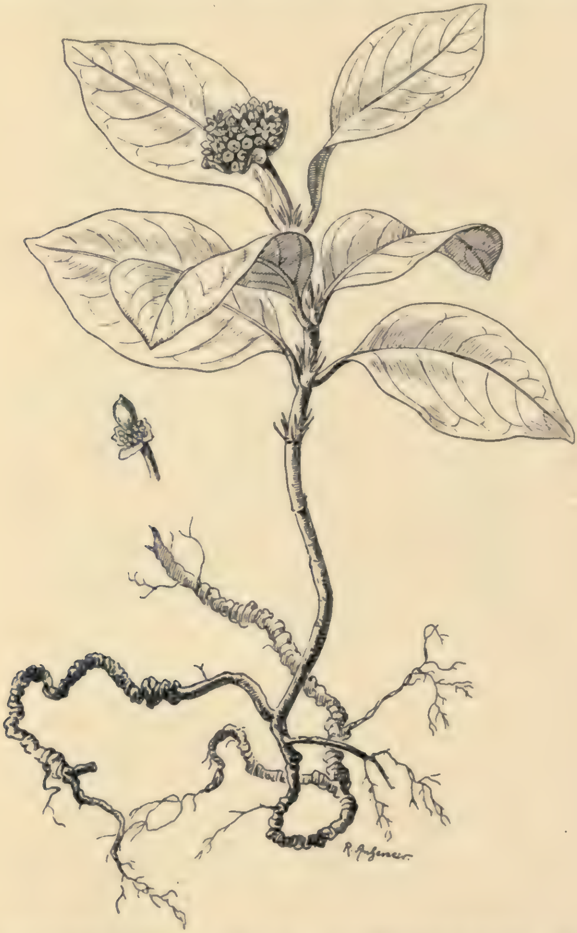


Fig. 754.—*Uragoga Ipecacuanha* (½ nat. size). Infrutescence by the side. *OFFICIAL.*

(*b*) *Lonicereae*, flowers zygomorphic, fruit a berry. The Honeysuckle (*Lonicera* *periclymenum*) is one of our native lianes. *Diervilla* (*Weigelia*) is a favourite flowering shrub.

Official.—*Sambucus nigra* yields SAMBUCI FLORES.

Family 3. **Valerianaceae.**—Herbs or small shrubs, with decussately arranged leaves and asymmetrical flowers. Calyx only developed with the fruit as a pappus. Corolla pentamerous, spurred. Stamens 4, 3, or 1. Carpels 3, but only one loculus of the ovary is fertile, and contains a single, pendulous ovule (Figs. 757, 758).

Genera.—*Valeriana*, Valerian. *V. officinalis* is a herbaceous plant widely distributed throughout Europe. It has a short, thick, chambered rhizome, which often sends out subterranean offsets. Leaves imparipinnate. Inflorescence a panicle. Spur short. The hairy calyx developed on the single-seeded fruit assists in its dispersal by the wind. *Valerianella*, small, inconspicuous plants. *V. olitoria*, Lamb's Lettuce. *Centranthus ruber* from the Mediterranean region has a long spur to the flower; it is commonly cultivated in gardens.

Official. — *Valeriana officinalis* yields VALERIANAE RHIZOMA.

Order 8. Campanulinae

Herbs, with simple, entire, alternate, exstipulate leaves. Floral formula usually K 5, C (5), A 5, G (2-3); in other cases there are 5 carpels. A well-developed calyx, and stamens inserted on the floral axis with their anthers coherent are characteristic of the order.

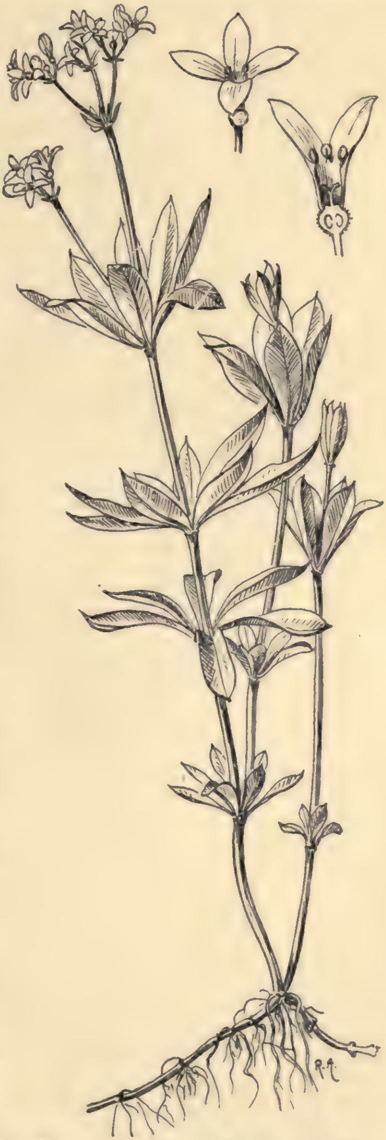


Fig. 755.—*Asperula odorata* (⅔ nat. size). Single flower and flower in longitudinal section (enlarged).

Family 1. **Campanulaceae.**—Herbs with milky juice; flowers actinomorphic; ovary as a rule trilocular. Fruit a capsule (Figs. 759, 760).

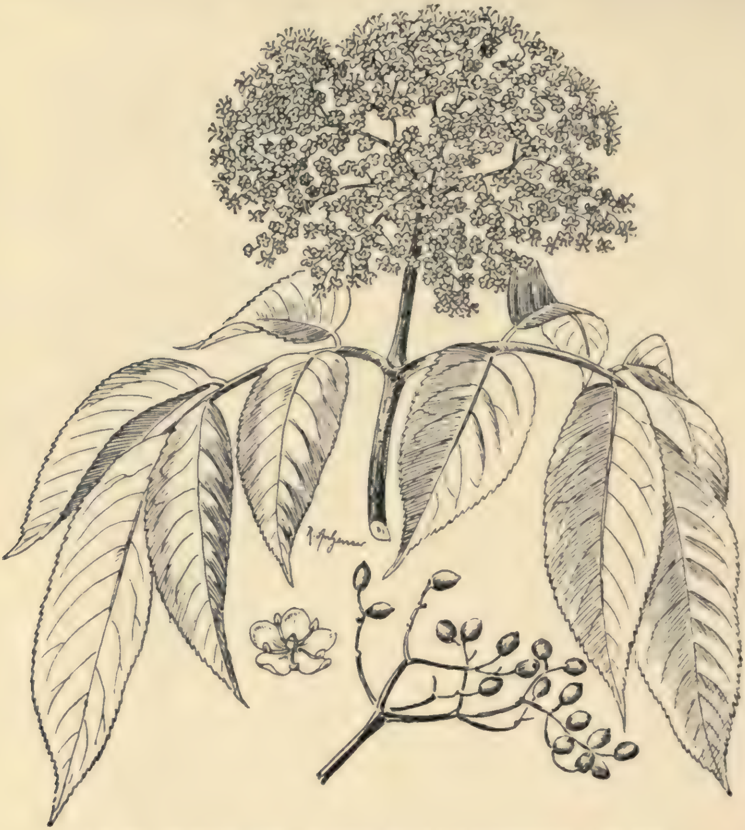


Fig. 756.—*Sambucus nigra.* Flowering shoot and infrutescence (½ nat. size). Single flower (enlarged). *OFFICIAL.*

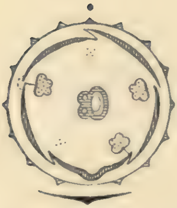


Fig. 757.—*Valeriana.* Floral diagram.

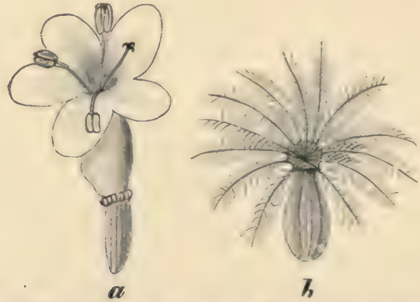


Fig. 758.—*Valeriana officinalis.* *a*, Flower (× 8); *b*, fruit (× 4). *OFFICIAL.*

BRITISH GENERA ([59]).—*Campanula,* numerous species with showy flowers. *Phyteuma,* with spike-like inflorescences. The petals separate at the base, remaining united at the tip until the pollen, which is shed in the bud, is swept out by the hairs on the style; after this the lobes of the stigma, which until now have been closed, expand. *Jasione* resembles the Compositae in having its flowers in heads and its anthers united to form a tube.

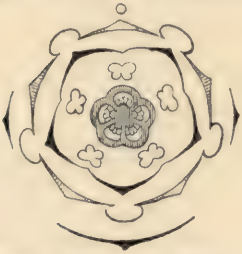


FIG. 759.—Floral diagram of *Campanula medium.* (After EICHLER.)

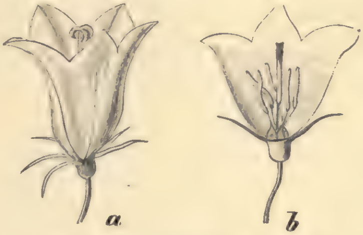


FIG. 760.—*Campanula rotundifolia.* *a,* Flower; *b,* the same cut through longitudinally. (Nat. size.)

Family 2. **Lobeliaceae.**—Herbs with milky juice, closely related to the Campanulaceae. Flowers zygomorphic; carpels 2. The median sepal is anterior and comes below a deep incision in the corolla. The normal position is assumed by torsion of the whole flower through 180° or inversion of the flower; these methods also occur in the Orchidaceae (Fig. 761). In Britain *Lobelia Dortmanna,* an aquatic plant of northern regions which reaches its southern limit in the north of Germany.

OFFICIAL.—*Lobelia inflata* from N. America (Fig. 762) yields LOBELIA.

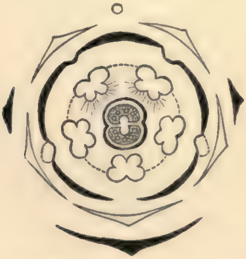


FIG. 761.—Floral diagram of *Lobelia fulgens.* (After EICHLER.)

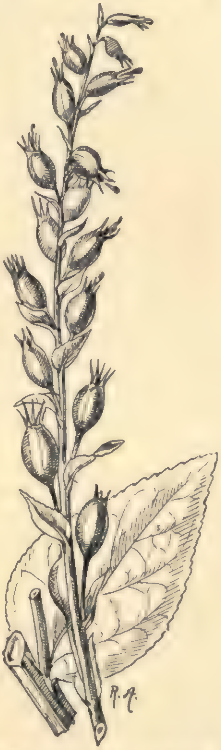


FIG. 762.—*Lobelia inflata* ($\frac{2}{3}$ nat. size). *OFFICIAL.*

Family 3. **Cucurbitaceae** ([60]).—Herbs, without milky juice, climbing by means of tendrils; the cordate or palmately lobed leaves bear coarse hairs. Flowers diclinous; monœcious or less commonly diœcious. Calyx and corolla adherent below. Anthers united in pairs or all coherent, ∽-shaped. Ovary trilocular. Fruit a berry, with a firm rind and six large, succulent, parietal placentas.

IMPORTANT GENERA.—*Cucumis sativus*, the Cucumber, and *C. Melo*, the Melon, are commonly cultivated. Tendrils unbranched; the tendril corresponds to a bract and arises nearer to the apex of the shoot than the leaf nearly opposite to which it stands. The female flowers are solitary, the male are grouped in small inflorescences, in the axils of the leaves. As has been shown by NOLL, fertilisation is not a necessary preliminary to the development of the fruit of the Cucumber. *Cucurbita pepo*, the Pumpkin, has branched tendrils, which represent axillary shoots of the simple tendrils. Each branch of the tendril corresponds to a leaf of the shoot, and may sometimes subtend an axillary bud. Both male and female flowers are solitary in the leaf-axils. *Bryonia*, the Bryony, is British (Fig. 764); it is poisonous and has thick, swollen, fleshy roots, long unbranched tendrils, and axillary inflorescences (11a). *Citrullus Colocynthis* is a perennial plant inhabiting the Asiatic and African deserts north of the equator. Leaves deeply three lobed and pinnately divided. Tendrils simple or forked; male and female flowers solitary in the axils of the leaves. The fruit is a dry berry (Fig. 765).

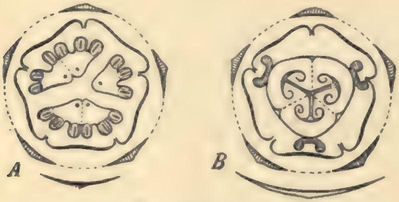


FIG. 763.—*Ecballium* (Cucurbitaceae). Diagram of a male (*A*) and of a female flower (*B*). (After EICHLER.)

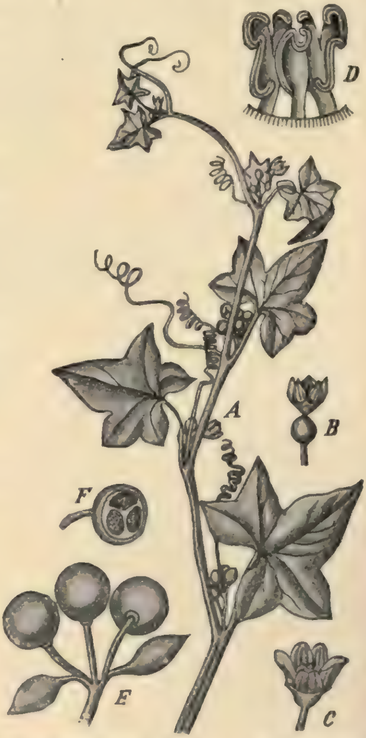


FIG. 764.—*Bryonia dioica.* *A*, Flowering branch (reduced); *B*, female, *C*, male flower (nat. size); *D*, androecium (magnified); *E*, fruits; *F*, fruit in section. *POISONOUS.*

OFFICIAL.—*Citrullus colocynthis* yields COLOCYNTHIDIS PULPA. ELATERIUM from *Ecballium elaterium*.

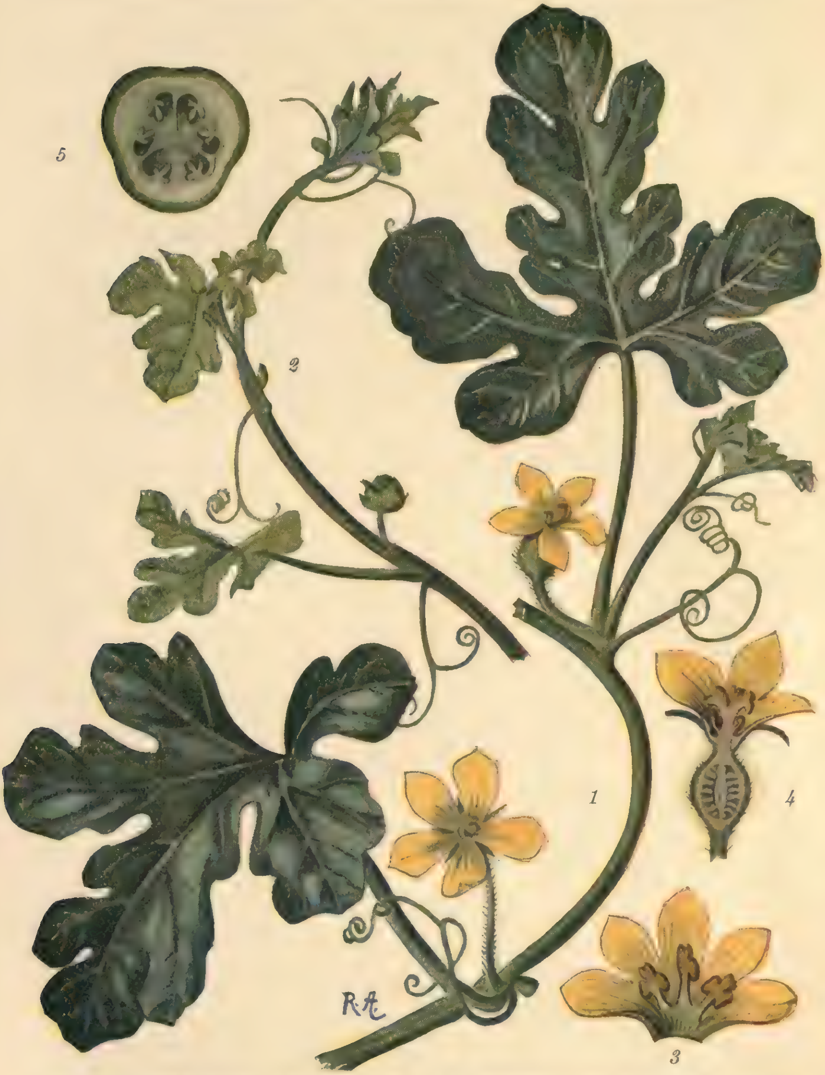


FIG. 765.—*Citrullus colocynthis* (½ nat. size). *1*, Shoot with male and female flowers. *2*, Apex of a shoot with a male flower-bud and tendrils. *3*, Male flower with corolla spread out. *4*, Female flower cut through longitudinally. *5*, Young fruit cut transversely. *OFFICIAL.*

Order 9. Aggregatae

For the most part herbs with the flowers in heads, surrounded by a common involucre. In relation to this the calyx of the individual flowers is reduced. Stamens epipetalous. Ovary inferior, unilocular with a single ovule. Fruit indehiscent.

Family 1. **Dipsacaceae.**—Herbs with opposite leaves. Flower with an epicalyx which persists on the fruit. Tetramerous or pentamerous. Stamens 4, anthers free. Ovule pendulous, anatropous. Seed with endosperm.

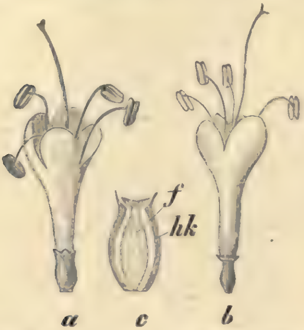


FIG. 766.—*Succisa pratensis.* *a*, Flower with epicalyx; *b*, the same after removal of epicalyx; *c*, fruit in longitudinal section; *f*, ovary; *hk*, epicalyx.

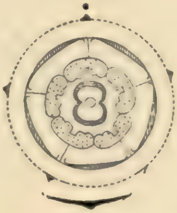


FIG. 767.—Compositae. Floral diagram (*Carduus*).

IMPORTANT GENERA.—*Dipsacus*, the Teazel, has recurved hooks on the involucral and floral bracts. The capitula of *D. fullonum* are employed in the carding of woollen cloth. Corolla with four lobes. *Succisa* (Fig. 766) has a four-lobed corolla; bracts are present on the common receptacle. *Scabiosa* has similar bracts but has pentamerous flowers; the marginal flowers of the head are larger and dorsiventral. It is cultivated as an ornamental plant. *Knautia* has tetramerous flowers; no floral bracts.

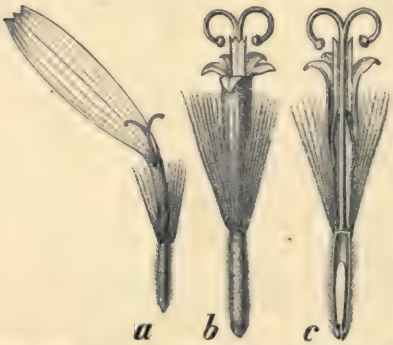


FIG. 768.—*Arnica montana.* *a*, Ray-flower; *b*, disc-flower; *c*, the latter cut through longitudinally. (After BERG and SCHMIDT, magnified.)

Family 2. **Compositae** (61).—For the most part herbs of very various habit; some tropical forms are shrubs or trees. Flowers actinomorphic or zygomorphic with no epicalyx. Stamens five; anthers introrse, cohering by their cuticles to form a tube which is closed below by the unexpanded stigma. The pollen is shed into the tube formed by the anthers and is swept out by the brush-like hairs of the style as the latter elongates. The style is bifid above. Ovule erect, anatropous (Fig. 770). Seed exalbuminous. The fruits are achenes, often bearing at the upper end a crown of hairs, the pappus. This corresponds to the calyx and aids in the dispersion of the fruit by the wind (Figs. 767-773). The replacement of reserve starch by inulin is characteristic of the Compositae.

The individual flowers are either radially symmetrical with a five-lobed corolla (Fig. 768 *b*, *c*) or they are two-lipped as in the South American Mutisieae, the upper lip having two teeth, the lower three. By suppression of the upper lip flowers with a single lip are derived; such flowers exhibit three teeth at the tip (Fig. 768 *a*). The ligulate flowers (*e.g.* of *Taraxacum*, Fig. 775) are similar in general appearance to the latter; the corolla is here deeply split on one side and its margin bears five teeth. In addition to those Compositae which have only ligulate or only tubular florets in the head, there are many which have tubular florets (disc-florets) in the centre, surrounded by one-lipped florets (ray-florets) (Fig. 769 *b*). These usually differ from one another in sex as well as in colour; the disc-florets are hermaphrodite, the ray-florets purely female. The flower-heads are thus heterogamous (*Matricaria, Arnica*). Lastly, the marginal florets may be completely sterile (*Centaurea Cyanus*) and serve only to render the capitulum conspicuous to insects.

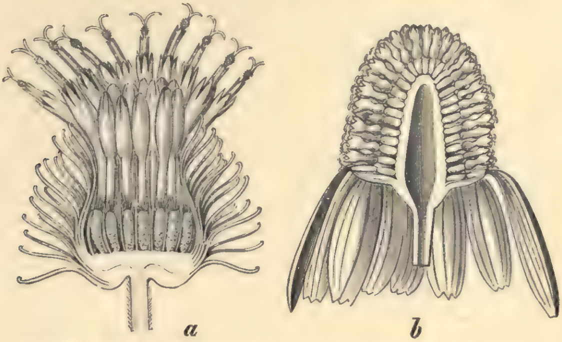


FIG. 769.—Longitudinal section of capitulum—*a*, of *Lappa major* with floral bracts; *b*, of *Matricaria Chamomilla* without floral bracts. (After BERG and SCHMIDT, magnified.)

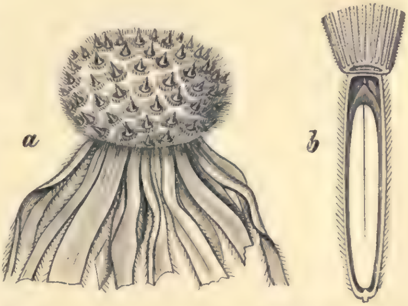


FIG. 770.—*Arnica montana*. *a*, Receptacle of capitulum after removal of fruit; *b*, fruit in longitudinal section, the pappus only partly shown. (After BERG and SCHMIDT, magnified.)

Important sub-families and genera. 1. *Tubuliflorae*, the heads contain only tubular florets: (*a*) *Cynareae*. The enlarged axis of the inflorescence or common receptacle has setaceous floral bracts; the involucral leaves form several series and are prickly or have membranous margins. The flowers are either all hermaphrodite or the marginal florets are sterile. Style swollen below the stigmas into a cushion-like ring. Fruits with a pappus. *Carduus* (Plumeless Thistle), pappus of simple, hair-like bristles. *Cirsium*, with feathery pappus. *Echinops*, with single-flowered capitula associated in numbers. *Lappa* (Burdock), involucral bracts with recurved, hook-like tips (Fig. 769 *a*). *Cynara Scolymus* (Artichoke). *Cnicus benedictus* (Fig. 774), capitula solitary, terminal, surrounded by foliage leaves. Involucral bracts with a large, sometimes pinnate, terminal spine and a felt of hairs. Marginal florets sterile. Pappus double. *Centaurea* with dry, scaly involucral bracts and large, sterile marginal florets. On the irritability of the stamens cf. Fig. 238 and p. 296.

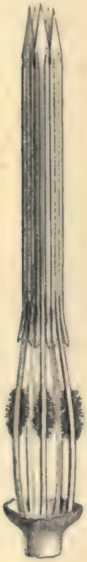


Fig. 771. — Androecium of *Carduus crispus* (× 10). (After Baillon.)

(*b*) ***Eupatorieae.*** Flowers hermaphrodite. Receptacle without floral bracts. Involucral leaves herbaceous. *Eupatorium cannabinum* (British). *Aggeratum mexicanum*, commonly cultivated.

2. ***Labiatiflorae. Mutisieae*** occur in tropical America.

3. ***Liguliflorae. Cichorieae*** with only zygomorphic, ligulate, florets with a five-toothed corolla in the flower-head. All the flowers are hermaphrodite. Laticiferous vessels in all organs of the plant. *Taraxacum officinale* (Dandelion, Fig. 775) is a common plant throughout the northern hemisphere. It has a long, carrot-shaped tap-root, a rosette of coarsely toothed leaves, and terminal inflorescences, borne singly on hollow stalks (apogamy, cf. p. 518). Fruits with an elongated beak, carrying up the pappus as a stalked, umbrella-shaped crown of hairs (Fig. 773). *Lactuca sativa*, Lettuce. *L. virosa*, a herbaceous plant of considerable height with a branched stem, sessile sagittate leaves and numerous, small, few-flowered inflorescences grouped in panicles. Fruits like those of *Taraxacum*. *L. Scariola* (62), Compass plant, has leaves which take a vertical position. *Cichorium Intybus* (Chicory), *C. endivia*, Endive, with heads of blue flowers; pappus of short erect scales (Fig. 772 C). *Tragopogon* and *Scorzonera* have a feathery pappus; *Sc. hispanica*. *Crepis* has a soft, flexible, hairy pappus of brownish colour. *Sonchus*, pappus of several series of bristles. *Hieracium* (63), a large European genus with many forms. (Apogamy and apospory, cf. p. 517.) Pappus white, rigid, and brittle (Fig. 772 B).

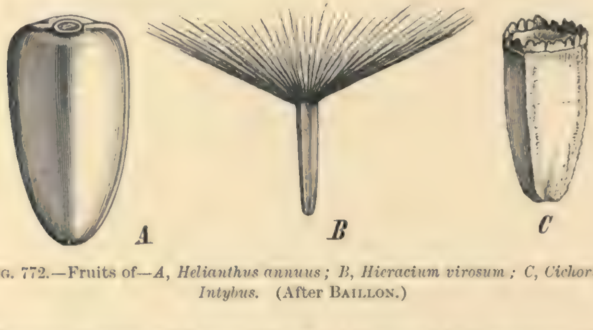


Fig. 772.—Fruits of—*A*, *Helianthus annuus*; *B*, *Hieracium virosum*; *C*, *Cichorium Intybus*. (After Baillon.)

4. *Diversiflorae.* Two distinct types of flower or flowers of distinct sexes in the capitulum.

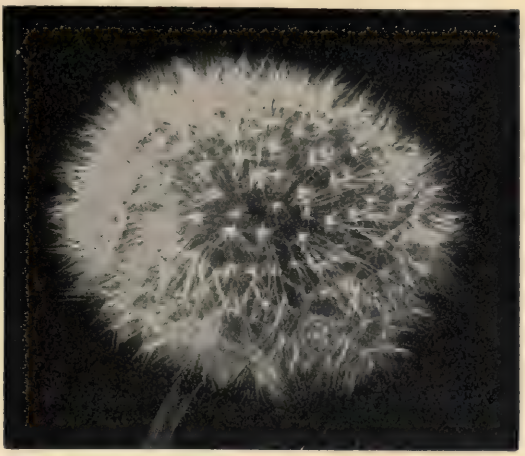


FIG. 773.—Head of fruits of *Taraxacum officinale*. The pappus is raised on a stalk-like prolongation of the fruit. (Nat. size.)

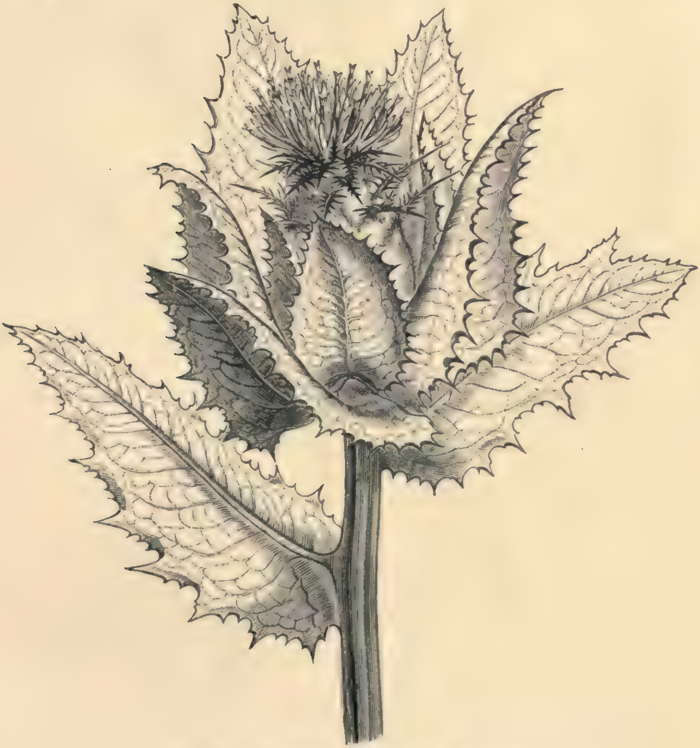


FIG. 774.—*Cnicus benedictus*. (After BAILLON.)

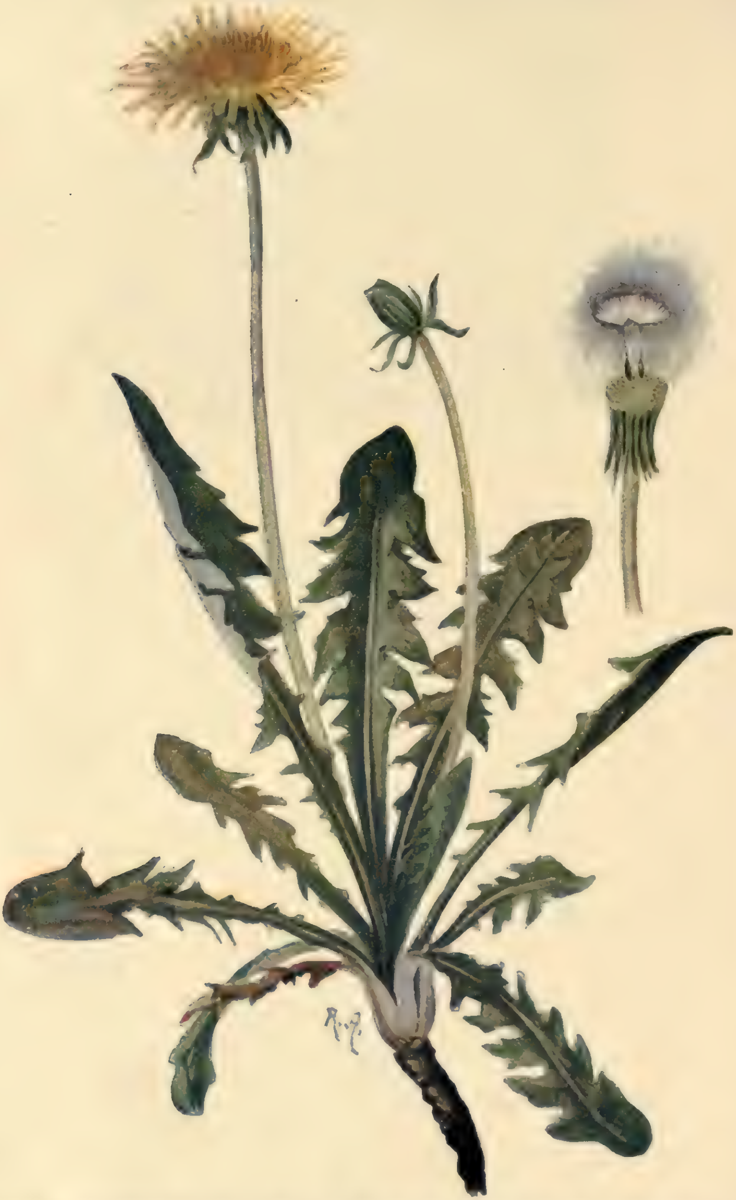


FIG. 775.—*Taraxacum officinale* (½ nat. size). By the side is a receptacle still bearing two of the fruits ; the pappus is raised on a stalk-like beak of the fruit. *OFFICIAL.*

(*a*) *Astereae*, receptacle naked, without floral bracts. Involucral bracts, numerous, imbricate. Hermaphrodite tubular flowers in centre, surrounded by one-

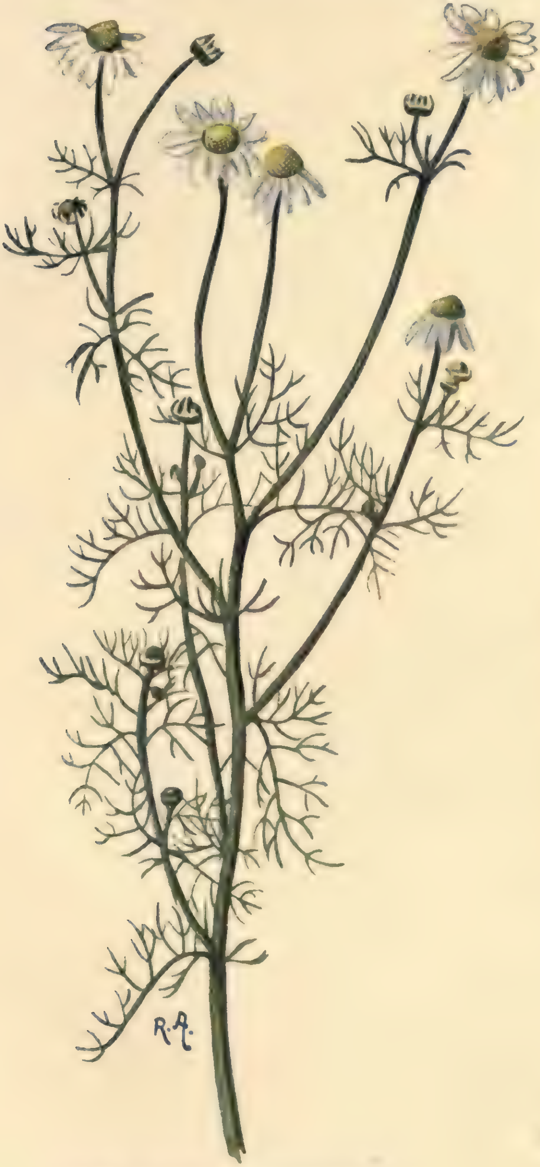


FIG. 776.—*Matricaria Chamomilla* (⅔ nat. size).

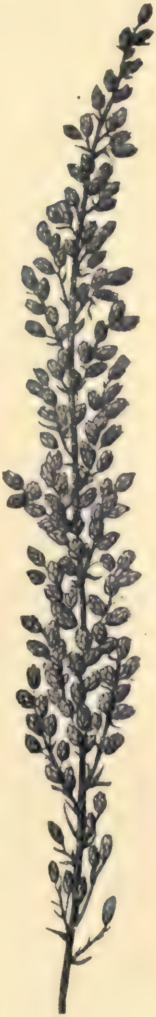


FIG. 777. — *Artemisia Cina*. (After SCHUMANN and ARTHUR MEYER.)

lipped ray-florets. Pappus as a rule of bristle-like hairs. Style with straight branches; stigmas terminal. Numerous species of *Aster*, *Solidago*, and *Erigeron* occur in Europe, America, and Asia. Species of *Aster* are cultivated. *Baccharis* (^{64}), shrubby diœcious plants from America. Species of *Haastia* (^{65}) are cushion-shaped plants with woolly hairs in New Zealand (Vegetable Sheep).

(*b*) *Inuleae* resemble the preceding group but have tailed anthers. Involucral leaves frequently dry and membranous. *Inula* occurs in Britain; *I. helenium* is cultivated. In *Gnaphalium*, *Antennaria* (^{65a}), *Helichrysum* (Everlasting flowers), *Leontopodium* (Edelweiss), *Filago*, etc., the dry involucral bracts are coloured and have flat, expanded appendages; the flowers are all tubular but the marginal florets are female, the disc-florets hermaphrodite. *Raoulia* (^{66}) resembles *Haastia* in habit and in distribution (cf. Fig. 193). *Odontospermum pygmaeum* (Rose of Jericho) closes its involucral bracts over the fruits when dry and expands them when moistened.

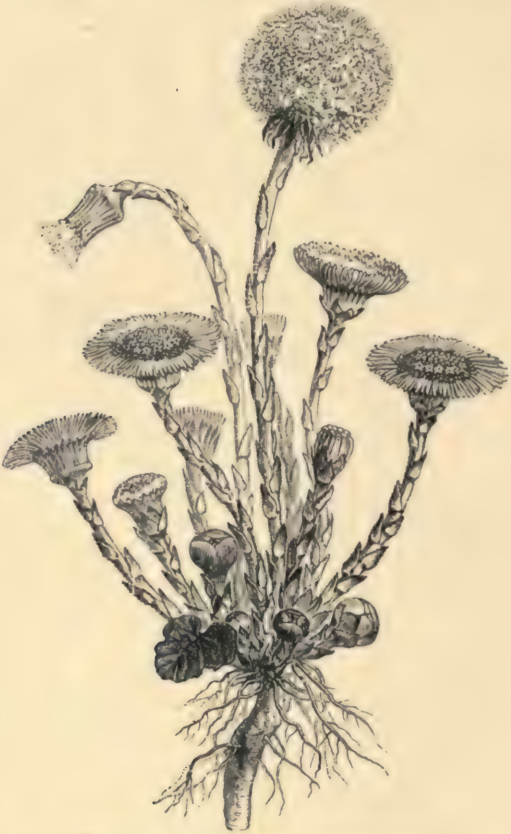


FIG. 778.—*Tussilago Farfara.* (After BAILLON.)

(*c*) *Heliantheae.* Receptacle with floral bracts. Involucral bracts herbaceous.

Disc-florets hermaphrodite, tubular. Ray-florets one-lipped, female, or hermaphrodite. Anthers without tails. Pappus wanting or formed of awns or scales. *Helianthus annuus* (Sunflower, Fig. 772 A), *H. tuberosus* (Jerusalem Artichoke), *Dahlia*, are all from America and in cultivation. In Britain *Bidens*; herbs with opposite leaves, sometimes heterophyllous. *Espeletia* (67), characteristic trees or herbs of the Pàramos of Colombia and Venezuela. *Tagetes*, *Zinnia*, ornamental plants from America.

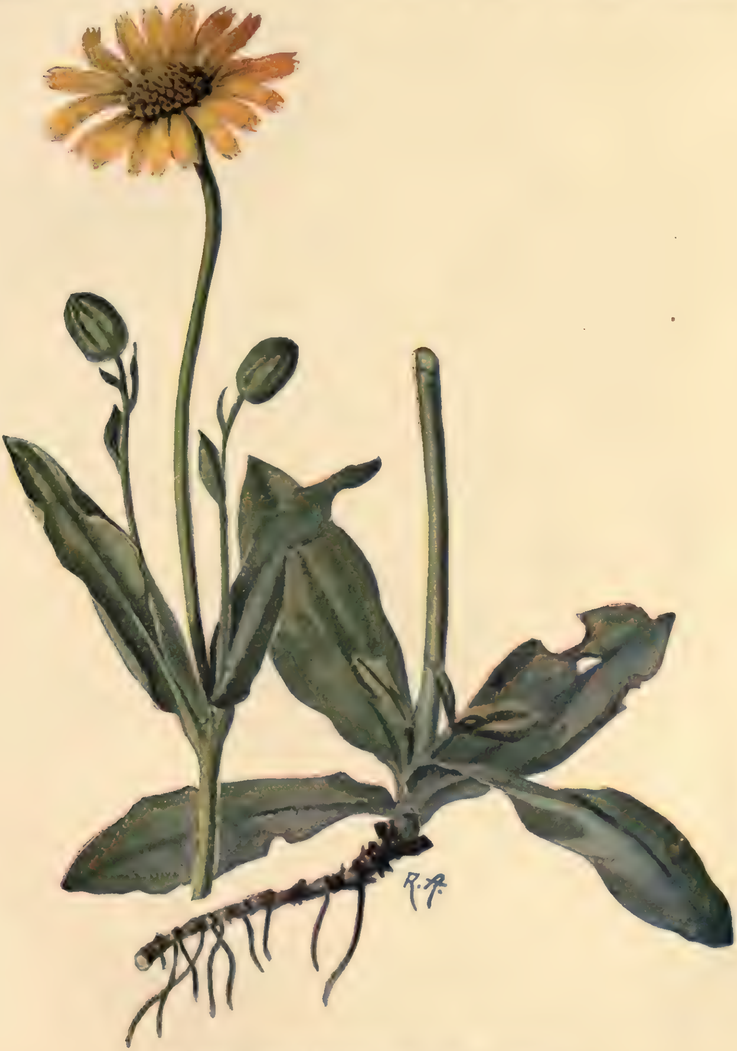


Fig. 779.—*Arnica montana* (½ nat. size). *OFFICIAL.*

(*d*) *Anthemideae.* Receptacle with or without floral bracts or hairs; involucral bracts with dry, membranous margins; in other respects like the preceding. *Achillea*, Milfoil; *Anthemis*, *Anacyclus*, with floral bracts. *Anthemis nobilis*, capitula composed of disc-florets only, or with these more or less replaced by irregular florets. *Anacyclus officinarum.* *Matricaria* has no floral bracts. *M. Chamomilla* (Chamomile, Figs. 769 b, 776) is an annual, copiously branched herb with a hollow, conical, common receptacle, yellow disc-florets and white, recurved, female ray-florets, in the terminal capitula. *Chrysanthemum*, *C. segetum*, *Tanacetum*, flowers all tubular, marginal florets female. *Artemisia* has all the florets tubular and usually the peripheral ones female (*A. Absinthium*, Wormwood); in the few-flowered capitula of *A. Cina* (Fig. 777) all the florets are hermaphrodite.

(*e*) *Senecioneae.* Receptacle naked, involucral bracts in one or two series. Pappus hairy, delicate, white; in other respects like the preceding. *Tussilago Farfara*, Coltsfoot, flowers appear before the leaves; the flowering stem bears scaly leaves and a single capitulum (Fig. 778). Female flowers at periphery in several series. Leaves large, cordate, thick, covered beneath with white hairs. *Petasites officinalis*, Butter-Bur. *Senecio*, plants of diverse habit, including some trees and succulent plants; of world-wide distribution. *S. vulgaris* has no ray-florets but only tubular, hermaphrodite florets. *Doronicum*, *Cineraria* are commonly cultivated. *Arnica montana* (Figs. 779, 768, 770) has a rosette of radical leaves in two to four opposite pairs and a terminal inflorescence bearing a single capitulum; from the axillary buds of the two opposite bracts one (rarely more) lateral inflorescence develops.

(*f*) *Calenduleae.* Fruits of the capitulum of varied and irregular shapes. *Calendula.*

OFFICIAL.—*Anacyclus Pyrethrum* yields PYRETHRI RADIX. SANTONINUM is prepared from *Artemisia maritima*, var. *Stechmanniana.* *Anthemis nobilis* yields ANTHEMEDIS FLORES. *Taraxacum officinale*, TARAXACI RADIX. *Arnica montana*, ARNICAE RHIZOMA.

Fossil Angiosperms (67)

The first undoubted Angiosperms appear in the Upper Cretaceous. They are represented by numerous species which, like the recent forms, can be divided into Monocotyledons and Dicotyledons. The most ancient forms are known only as leaves, so that their determination is a matter of difficulty. They agree essentially with living Angiosperms, and since they show no similarities to Gymnosperms or Pteridophytes, do not aid in bridging over the gap between the Angiosperms and these groups.

Of Monocotyledons examples of the Palmae are known from the Cretaceous period onwards. The leaves of Dicotyledons from the Cretaceous are doubtfully placed in various orders which contain the more lowly organised types (Querciflorae, Platanaceae); some are ascribed to *Eucalyptus.* The Angiosperms of the Eocene and the Oligocene can be determined with greater certainty; even in Northern Europe representatives of existing tropical and sub-tropical families occurred, *e.g.* Palmae, *Dracaena*, *Smilax* among Monocotyledons, numerous Querciflorae (esp. *Quercus*), Lauraceae (*Cinnamomum*, etc.), Leguminosae among Dicotyledons.

As the present period is approached the fossil Angiosperms throw even less light on the systematic arrangement of the group. The few genera that have become extinct (*e.g. Dryophyllum*, a supposed ancestral form of the Oaks) are wanting even in the Eocene. From the Miocene onwards the specific forms are in part identical with those now living, and in the Quaternary strata all the remains are of existing species. The general character of the Tertiary flora in Europe was, however, very different from that of the present day. It had the aspect of the flora of a much warmer region, and (as in the case of the Gymnosperms) contained forms which now exist only in distant regions.

INDEX OF LITERATURE

INTRODUCTION AND MORPHOLOGY

(1) E. Haeckel, Generelle Morphologie der Organismen, 1866, p. 52. (2) Fritz Müller, Für Darwin, 1864. (3) Charles Darwin, On the Origin of Species by Means of Natural Selection, 1859. (4) Hugo de Vries, Die Mutationstheorie, 1901-1903. (5) Carl Nägeli, Mechanisch-physiologische Theorie der Abstammungslehre, 1883. Julius Sachs, Flora, vol. lxxxii. 1896, p. 173. (6) R. v. Wettstein, most recently in Handbuch der systematischen Botanik, 1901, p. 40. (7) Cf. John Butler-Burke in "Nature," 1905, pp. 78, 294, 492; this investigator's results have been widely published in the daily press. On the other side see especially the review by W. Roux, Wochenschrift über die Fortschritte und Bewegungen auf dem Gesamtgebiete der Wissenschaft und Technik, 1906, No. 8. (8) Another interpretation is given by K. Goebel, Organography of Plants, 1898-1901 [English translation, 1900-1905]. (9) K. Goebel, *loc. cit.* and Vergleichende Entwickelungsgeschichte der Pflanzenorgane, 1883; F. Pax, Allgemeine Morphologie der Pflanzen, 1890. (10) K. Goebel, Organography, vol. i. p. 19, vol. ii. p. 35. (11) K. Goebel, *loc. cit.* vol. i. p. 42. (12) K. Goebel, Biol. Zentralbl. vol. xxii. 1908, p. 388. (13) K. Goebel, Organography, vol. ii. p. 241. (14) A. W. Eichler, Zur Entwicklungsgeschichte des Blattes, 1865. (15) K. Goebel, Organography, vol. ii. p. 308. (16) M. Raciborski, Flora, vol. lxxxvii. 1900, p. 1. (17) v. Deinega, Flora, vol. lxxxv. 1898, p. 439. (18) Ann. du Jard. Bot. de Buitenzorg, vol. ii. 1893, p. 98. (19) K. Goebel, Organography, vol. ii. p. 350. (20) K. Goebel, Bot. Ztg. 1880, p. 753. (21) S. Schwendener, Mechanische Theorie der Blattstellungen, 1878, together with numerous papers in the Stzber. d. Akad. d. Wiss. zu Berlin. (22) Hans Winkler, Jahrb. f. wiss. Bot. vol. xxxvi. 1901, p. 1, and vol. xxxviii. 1903, p. 501; further literature in these papers. (23) Wiesner, Biol. Zentralbl. vol. xxiii. 1903, p. 209. (24) K. Goebel, Arb. d. bot. Inst. in Würzburg, vol. ii. 1882, pp. 357 ff., and Biol. Zentralbl. vol. xxii. 1902, p. 389. (25) Freidenfelt, Flora, vol. xci. 1902, p. 115. (26) Rostowzew, Flora, vol. xlviii. 1890, p. 155, and K. Goebel, Organography, vol. ii. p. 226. (27) A. F. W. Schimper, Die epiphytische Vegetation Amerikas, 1888. (28) Eug. Warming, most recently in Engler and Prantl, Nat. Pflanzenfamilien, 3. Teil, Abt. 2a, 1891, p. 2. (29) K. Goebel, Flora, vol. xcv. 1905, p. 165. (30) K. Goebel, Organography, vol. ii. p. 226. (31) Cytologische Studien aus dem Bonner botanischen Institut, Jahrb. f. wiss. Bot. vol. xxx. 1897, p. 155. Fr. Meves, Verhandl. d. Anat. Gesell., sechzehnte Vers., Halle, 1902, p. 152. M. Koernicke, Der heutige Stand der pflanzlichen Zellforschung., Ber. d.

deutsch. bot. Gesellsch. vol. xxi. (1903), p. 82. Koernicke, Centrosomen bei den Angiospermen? Flora, vol. xcvi. 1906, p. 501. (32) Cf. on the one hand Alfred Fischer, Untersuchungen über den Bau der Cyanophyceen und Bacterien, 1897, and Die Zelle der Cyanophyceen, Bot. Zeitg. vol. lxii. 1905, p. 51, and on the other F. G. Kohl, über die Organisation und Physiologie der Cyanophyceenzelle and Edgar W. Olive, Beihefte zum Bot. Zentralbl. vol. xviii. 1904, p. 9. (33) Hugo de Vries, Jahrb. f. wiss. Bot. vol. xvi. 1885, p. 465. (34) N. Gaidukov, Ber. d. deutsch. bot. Ges. 1906, p. 155. (35) Most recently Paul Kretzschmar, Jahrb. f. wiss. Bot. vol. xxxix. 1904, p. 273. (36) Fr. Meves has given the name of "chondromites" to thicker fibrils of peculiar nature which he has observed in certain cases in the cells which line the pollen-sacs. Ber. d. deutsch. Bot. Ges. 1904, p. 284. Cf. also Rudolf Beer, Beiheft zum bot. Zentralbl. vol. xix. 1905, p. 304, and G. Tischler, Jahrb. f. wiss. Bot. vol. xlii. 1906, p. 568. (37) Cf. on this subject especially Alfred Fischer, Fixierung, Färbung und Bau des Protoplasma, 1899, and Albert Degen, Bot. Ztg. 1905, Abt. I. p. 202. (38) Cf. the most recent works of Grégoire and his pupils as well as those of E. Strasburger. (39) Belajeff, Three papers on Spermatogenesis in the Ber. d. deutsch. bot. Ges. 1897, p. 337 ff.; Ikeno, Jahrb. f. wiss. Bot. vol. xxxii. 1898, p. 557; Hirase, Journal of the College of Science Tokyo, vol. xii. 1898, p. 105; Herbert J. Webber, Botanical Gazette, vol. xxiii. 1897, p. 453, vol. xxiv. 1897, p. 16 and p. 225; S. Ikeno, Beihefte zum bot. Zentralbl. vol. xv. 1903, p. 65. K. Miyake, Bot. Magaz. Tokyo, vol. xix. 1905, p. 98, and Ber. d. deutsch. bot. Gesell. 1906, p. 78. (40) A. F. W. Schimper, Jahrb. f. wiss. Bot. vol. xvi. 1885, p. 1, and Bot. Ztg. 1880, p. 886. (41) L. Marchlewski, Section Chlorophyll in vol. viii. of Roscoe-Schorlemmer, Organ. Chemie, 1901, p. 83; C. A. Schunk, Proceed. Roy. Soc. London, vol. lxv. 1900, p. 177, vol. lxviii. 1901, p. 474, and vol. lxxii. 1904, p. 165; also A. Tschirch, Ber. d. deutsch. bot. Gesell. 1904, p. 414. (42) Tschirch, Untersuch. üb. d. Chlorophyll, 1884. (43) L. Marchlewski, cf. in 41; also W. Küster, Ber. d. deutsch. bot. Gesell. 1904, p. 339; L. Marchlewski, *ibid.* 1906, p. 146. (44) Th. W. Engelmann, Bot. Ztg. 1882, p. 663; Hans Molisch, Bot. Ztg. 1905, Abt. I. p. 131. (45) Hans Molisch, in 44. (46) C. A. Schunk in the last edition of 41, p. 172; cf. Molisch, Ber. d. deutsch. bot. Gesell. 1896, p. 27; Tammes, Flora, vol. lxxxvii. 1902, p. 205, and Kohl, Unters. über d. Karotin, etc. 1902; A. Tschirch, in 41, p. 417. (47) Complete literature in Louis Gaucher, Étude générale sur la membrane cellulaire chez les végétaux, 1904. (48) Pféffer, Unters. aus dem bot. Inst. zu Tübingen, vol. i. 1885, p. 525; G. Haberlandt, Sinnesorgane im Pflanzenreich, 1901, p. 126. (49) W. Rothert, Anzeiger der Akad. d. Wiss. in Krakau, 1897, p. 11. (50) G. Haberlandt, Die Lichtsinnesorgane der Laubblätter, 1905. Cf. also H. R. von Guttenberg, Ber. d. deutsch. bot. Gesell. 1905, p. 265. (51) Numerous researches of Julius Wiesner, collected in his Anatomie und Physiologie der Pflanzen, edition iv. 1898, p. 39 ff. and p. 339. (52) Gilson, La cristall. de la cell. in La Cellule, vol. ix. 1893, p. 397. (53) L. Mangin, Journ. de Bot. vol. vii. 1893, pp. 37, 121, 325. Complete literature to 1904 in Louis Gaucher in 47. More recently Friedrich Czapek, Biochemie d. Pflanz. 1905, vol. i. p. 506. (54) Gilson, Rech. chim. sur la Membr. cell. des Champ. in La Cellule, vol. xi. 1894, p. 7. (55) Fr. Czapek in Hoppe-Seyler's Ztschr. f. physiol. Chemie, vol. xxvii. 1899, p. 141; Congrès internat. de Bot. Paris, 1900. (56) F. C. von Faber, Ber. d. deutsch. bot. Gesell. 1904, p. 177. (57) Van Wisselingh, Archives Néerland. vol. xxvi. 1892, and vol. xxxviii. 1894. (58) Cf. especially Z. Kamerling, Bot. Zentralbl. vol. lxxii. 1897, p. 85. (59) Klebs, Unters. aus dem bot. Inst. zu Tübingen, vol. i. 1885, p. 582. (60) Litera-

ture in ERNST KÜSTER, Pathol. Pflanzenanat. 1903, p. 10. (61) MOLISCH, Studien über Milchsaft und Schleimsaft der Pflanzen, 1901. (62) CARL NÄGELI, Die Stärkekörner, 1858. (63) A. F. W. SCHIMPER, Bot. Ztg. 1881, p. 223 ; ARTHUR MEYER, Unters. über die Stärkekörner, 1895 ; cf. also SYNIEWSKI, Bull. internat. de l'Acad. d. sc. de Cracovie, 1899, p. 245, who there criticises A. Meyer's distinction of two physical modifications of the substance of the starch-grain. (64) H. FISCHER, Beitr. z. Biol. d. Pfl. vol. viii. 1898, p. 53. (65) HENRY KRAEMER, Bot. Gazette, 1902, p. 341. (66) L. MAQUENNE and EUG. ROUX, Compt. rend. 1905, vol. cxl. p. 1303, and 1906, vol. cxlii. p. 95. (67) O. BÜTSCHLI, Verh. d. naturhist.-med. Ver. at Heidelberg, 1903, vol. xvii. p. 451. (68) A. TSCHIRCH and H. KRITZLER, Ber. d. deutsch. pharm. Gesell. 1900, vol. x. p. 214. (69) W. PFEFFER, Jahrb. f. wiss. Bot. vol. viii. 1872, p. 472. (70) A. ZIMMERMANN, Beitr. z. Morph. u. Phys. der Pflanzenzelle, vol. i. 1891, p. 113. (71) L. KNY, Ber. d. deutsch. bot. Gesell. 1887, p. 387. (72) M. RACIBORSKI, Anzeiger, Akad. Wiss. Krakau, 1893, p. 259. (73) A. TSCHIRCH, Ber. d. deutsch. Bot. Gesell. 1904, p. 419. (74) Cf. O. BÜTSCHLI in 67, pp. 436 and 506. (75) LEO ERRERA, L'épiplasme des Ascomycètes, 1882, and other papers. (76) G. BERTHOLD, Studien über Protoplasmamechanik, 1886, p. 24. (77) A. TSCHIRCH, Die Harze und die Harzbehälter, 1900. (78) R. CHODAT and A. BACH, Archives des sciences phys. et math. de Genève, 1904, etc.; then W. PALLADIN, Ber. d. deutsch. bot. Gesell. 1905, p. 240, 1906, p. 97 ; most recently T. KNASNOSSELSKY, in Ber. d. deutsch. bot. Gesell. 1906, p. 134. (79) M. RACIBORSKI, Ber. d. deutsch. bot. Gesell. 1898, pp. 52, 119, and Flora, 1898, p. 362. (80) WINOGRADSKY, Bot. Ztg. 1887, p. 493, and Beiträge zur Morph. und Phys. der Bakterien, 1888. (81) HANS MOLISCH, Bot. Ztg. 1905, Abt. I. p. 161. (82) On the botanical side the numerous works of E. STRASBURGER, M. TREUB, L. GUIGNARD, WL. BELAJEFF, J. BRETLAND FARMER, NĚMEC, V. GREGOIRE, BERGHS, ROSENBERG, ALLEN, MIYAKE, J. B. OVERTON and others. (83) TH. BOVERI, Ergebnisse über die Konstitution der chromatischen Substanz des Zellkerns, 1904 ; V. GRÉGOIRE and A. WYGAERTS, Beihefte z. bot. Zentralbl. vol. xiv. 1903, p. 18. (84) E. STRASBURGER, ALLEN, MIYAKE, J. B. OVERTON, Jahrb. f. wiss. Bot. vol. xlii. 1906, p. 1 ; the various investigations on the nature of the reduction of chromosomes should be compared in the works of the authors mentioned in 82. (85) HARPER, SWINGLE, STRASBURGER, Jahrb. f. wiss. Bot. vol. xxx. 1897 ; MOTTIER, Ber. d. deutsch. bot. Gesell. 1898, p. 124 ; MOORE, *ibid.* p. 266. (86) R. A. HARPER, Jahrb. f. wiss. Bot. vol. xxx. 1897, p. 249. (87) On the botanical side numerous works especially of G. THURET, N. PRINGSHEIM, E. STRASBURGER, L. GUIGNARD, NAWASCHIN, and others. (88) Especially the works of WL. BELAJEFF, most recently in Ber. d. deutsch. bot. Gesell. 1897, p. 337 ff. (89) The works cited under 39 by IKENO, HIRASE, J. WEBBER, and K. MIYAKE. (90) E. STRASBURGER, Jahrb. f. wiss. Bot. vol. xli. 1905, p. 88. (91) JUEL, Botan. Zentralbl. vol. lxxiv. 1898, p. 369. Abh. d. Kl. Schwed. Akad. d. Wiss. vol. xxxiii. 1900, No. 5. (92) SW. MURBECK, Lunds Univ. Arskrift, vol. xxxvi. Afd. II. No. 7 ; Kongl. Fysiogr. Sällsk. Handlingar, vol. xi. No. 7, 1901 ; E. STRASBURGER in 90. (93) JAMES BERTRAM OVERTON, Bot. Gazette, vol. xxxiii. 1902, p. 363. (94) C. RAUNKIAER, Archiv für Botanik, vol. ii. N. 4, p. 7 ; O. JUEL, Botan. Tidsskr. vol. xxv. 1903, p. 109. (95) C. H. OSTENFELD and C. RAUNKIAER, Bot. Tidsskr. vol. xxv. 1903, p. 409, and Ber. d. deutsch. bot. Gesell. 1904, p. 376 ; O. ROSENBERG, *ibid.* 1906, p. 157. (96) AL. BRAUN, Abhandl. d. Berl. Akad. 1856, p. 337 ; A. DE BARY, Bot. Ztg. 1857, p. 379. (97) SHAW, Bot. Gazette, vol. xxiv. 1897, p. 114 ; ALEX. NATHANSOHN, Ber. d. deutsch. bot. Gesell. 1900, p. 99. (98) Of the copious literature there need

only be mentioned Arthur Meyer, in Bot. Ztg. 1896, Abt. I. p. 187, and Ber. d. deutsch. bot. Gesell. 1897, p. 166 ; W. Gardiner, continued in recent years of the Proc. of the Roy. Soc. London, and Proc. of the Cambridge Phil. Soc.; E. Strasburger, Jahrb. f. wiss. Bot. vol. xxxvi. 1901, p. 493, the whole literature is given in this paper ; Arthur W. Hill, Phil. Trans. Roy. Soc. London, vol. cxciv. 1901, p. 83, and Annals of Botany, vol. xv. 1901, p. 575. (99) A. de Bary, Vgl. Anat. d. Vegetationsorgane, 1877 [Translated. Comparative Anatomy of the Phanerogams and Ferns] ; G. Haberlandt, Physiol. Pflanzenanat. 3rd edition, 1896 ; H. Solereder, Syst. Anat. d. Dicotyledonen, 1899. (100) Henri Devaux, Mém. de la Soc. des Sc. phys. et nat. de Bordeaux, vol. iii. 1903, p. 89. (101) H. Kroemer, Bibl. Bot. Heft 59, 1903, p. 20. (102) G. Haberlandt in 50. (103) E. Strasburger, Jahrb. f. wiss. Bot. vol. v. 1866, p. 297 ; S. Schwendener, Monatsber. d. Berl. Akad. d. Wiss. 1881, p. 883, etc. (104) G. Haberlandt, Phys. Pflanzenanat. 3rd edition, 1896, p. 430, Bot. Unters. Schwendener, dargebracht, 1899, p. 104. (105) Haberlandt, Sinnesorgane im Pflanzenreich, 1901. (106) A. Nestler, Ber. d. deutsch. bot. Ges. 1900, pp. 189, 327 ; Peters, Stzber. d. Niederrh. Gesell. Bonn, Med. Sekt. 1900, p. 33. (107) In 101, p. 26. (108) Cf. N. Wille, Beiträge zur physiol. Anat. der Laminariaceen, 1897. (109) A. G. Tansley and Edith Chick, Annals of Botany, vol. xv. 1901, p. 13. (110) in 104, p. 308. (111) F. C. von Faber, Ber. d. deutsch. bot. Gesell. 1904, p. 296. (112) Alfred Fischer, Studien über die Siebröhren der Dikotylenblätter, 1885 ; E. Strasburger, über den Bau und die Verrichtung der Leitungsbahnen in den Pflanzen, 1891, pp. 98, 297. (113) Ph. van Tieghem, Traité de Botanique, édition 2, 1891, p. 737 ; Strasburger, the work cited under 112 ; J. C. Schoute, Die Stelartheorie, 1902. (114) Against the Stelar Theory cf. especially Solms-Laubach, Bot. Ztg. 1903, Abt. II. pp. 37, 147. (115) Haberlandt, Jahrb. f. wiss. Bot. vol. xxxviii. 1902, p. 450. (116) in 56, p. 181. (117) G. Haberlandt, in 104, p. 244. (118) C. Sauvageau, M. von Minden, P. Weinrowski, cf. in G. Haberlandt, Physiol. Pflanzenanatomie, 3rd edition, 1904, pp. 437, 475. (119) In Nägeli, Beiträge zur wiss. Bot. Heft I. 1858, and especially in the work of De Bary, cited in 99, p. 243 ff. (120) Literature in A. Gravis, Mém. publ. par. l'Acad. roy. de Belgique, vol. lvii. 1898 ; R. Sterckx, Arch. Inst. bôt. univ. Liège, vol. ii. 1900. (121) J. C. Schoute, Flora, vol. xcii. 1903, p. 32. (122) W. Eichler, Sitzber. d. Berl. Akad. d. Wiss. vol. xxviii. 1886, p. 501. M. Barsickow, Verh. d. phys. med. Ges. zu Würzburg, 1901, vol. xxxv. p. 213. (123) Especially the works of De Bary cited under 99, of E. Strasburger under 112, of Haberlandt under 99, and the works of Burgerstein in the publications of the Wien. Akad. (124) J. C. Schoute, Verhandl. d. Koninkl. Akad. van Wetensch. Amsterdam, Tweede Sectie, Deel IX. No. 4, 1902. Schoute terms a cambium active on both sides dipleuric, to one side only monopleuric ; a cambium with a single initial layer is spoken of as initial cambium in contrast to stratified cambium proceeding from several contributory layers. (125) H. Mayr, Zeitschr. f. Forst- u. Jagdwesen, vol. xxv. 1893, pp. 313, etc. (126) Alfred Fischer, Jahrb. f. wiss. Bot. vol. xxii. 1890, p. 73. E. Strasburger in 112, p. 883 ff. (127) L. Kny, Ber. d. deutsch. bot. Gesell. 1890, p. 176, and E. Strasburger under 112. (128) Especially Ph. van Tieghem, Traité de Botanique, 2nd edition, 1891, p. 719. Also I. Freidenfelt, Flora, vol. xci. 1902, p. 115, and M. Büsgen, Flora, vol. xcv. 1905, p. 58. (129) Especially H. Schenck, Beiträge zur Biologie und Anatomie der Lianen, 1892. (130) A. B. Frank, Die Krankheiten der Pflanzen, 2nd edition, 1895, vol. i. p. 81 ; Küster in 143. (131) J. C. Schoute under 124. (132) A. B. Frank, Bot. Ztg. 1864, p. 186 ; G. Kraus, Abh. d. naturf. Ges. zu Halle, vol. xvi. 1885, p. 365 ;

E. Strasburger in 112, p. 107 ; R. Meissner, Bot. Ztg. Abt. I. 1894, p. 55, and 1901, p. 25. (133) Especially De Bary in 99, p. 560 ; Damm, Beihefte z. bot. Zentralbl. vol. xi. 1901, p. 222. (134) Hannig, Bot. Ztg. Abt. I. 1898, p. 24. (135) Stahl, Bot. Ztg. 1873, p. 561 ; H. Devaux, Ann. des sc. nat. Bot. sér. 8, 1900, vol. xii. p. 1 ; literature in Haberlandt in 99, p. 419. (136) H. v. Mohl, Bot. Ztg. 1860, pp. 1, 132, 273 ; v. Bretfeld, Jahrb. f. wiss. Bot. vol. xii. 1879-81, p. 133 ; Van Tieghem, Traité de Bot., édition 2, 1891, vol. i. p. 865 ; Staby, Flora, 1886, p. 158 ; Tisson, Mém. de la Soc. Linn. de Normandie, vol. xx. 1900. (137) Cf. especially J. Wiesner, Ber. d. deutsch. bot. Gesell. 1906, p. 32. (138) Literature in the work of Küster cited under 143. (139) Cf. B. Němec, Studien über die Regeneration, 1905. More recently W. Figdor, Ber. d. deutsch. bot. Gesell. 1906, p. 13. (140) Henri Devaux, Actes de la Soc. Linn. de Bordeaux, sér. 6, vol. viii. 1903, p. 98. (141) Otto Appel, Ber. d. deutsch. bot. Gesell. 1906, p. 118. (142) A. Tison, Bull. de la Soc. Linnéenne de Normandie, sér. 5, vol. viii. 1904, p. 176. (143) Hans Winkler, Ber. d. deutsch. bot. Gesell. 1902, p. 81 ; K. Goebel, Biol. Zentralbl. vol. xxii. 1902, p. 385 ; Flora, vol. xcii. 1903, p. 132 ; Ernst Küster, Pathologische Pflanzenanatomie, 1903, p. 8 ; Fr. Hildebrand, Ber. d. deutsch. bot. Gesell. 1906, p. 39. (144) H. Leitgeb, Untersuchungen über die Lebermoose, 6. Heft, 1881. (145) Auguste Pyrame de Candolle, Théorie élémentaire de la Botanique. (146) E. de Wildeman, Mémoires couronnés, etc. publiés par l'Acad. de science de Belgique, 1898, vol. liii. (147) H. Leitgeb in 144, 3. Heft 1877 ; this includes the literature. (148) W. Hofmeister, Die Lehre von der Pflanzenzelle, 1867, p. 135 ; includes the older literature ; later in numerous special papers by Leitgeb ; on Equisetum cf. also E. Strasburger, Bot. Praktikum, edition 4, p. 312, includes literature. (149) J. Sachs, Arbeiten des Bot. Inst. in Würzburg, vol. ii. 1878 and 1879, pp. 46, 185. (150) Johannes Hanstein, Festschr. d. niederrh. Gesell. f. Natur- und Heilkunde, 1868, p. 109. (151) L. Errera, Bull. de la soc. Belge de Microscopie, vol. xiii. p. 12, 1886 ; and in 60. Vers. Naturforscher u. Ärzte zu Wiesbaden, Biol. Zentralbl. 1887-88, p. 728 ; Berthold, Studien über Protoplasmamechanik, 1886, p. 219 ; cf. also De Wildeman in 146. (152) C. Nägeli and Leitgeb, Beitr. z. wiss. Bot. von C. Nägeli, 4. Heft, 1868, p. 73. (153) Rostowzew, Flora, vol. xlviii. 1890, p. 155. (154) Especially E. v. Janczewski, Ann. des sc. nat. Bot. sér. 5, vol. xx. 1874, pp. 162, 208, and Ph. van Tieghem, Traité de Bot. 2nd edition, 1891, p. 694, where the literature is given. (155) K. Goebel, Organography of Plants, vol. ii. p. 242. (156) Ludwig Koch, Jahrb. f. wiss. Bot. vol. xxv. 1893, p. 380. (157) Especially Ph. van Tieghem in 154, p. 700, where the literature is given. (158) K. Goebel, Organography of Plants, vol. i. p. 141. (159) The most important literature will be found in the works of A. Weismann, Th. Boveri, E. Strasburger. (160) Especially O. Penzig, Pflanzen-Teratologie, 1890, where the literature will be found ; K. Goebel, Organography of Plants, vol. i. p. 177. Ernst Küster in 143 ; Werner Magnus, Ber. d. deutsch. bot. Gesell. 1903, p. 129. Ernst Küster terms abnormal development of the cell contents or of the thickening of the wall of the cells metaplasy, excessive division of cells hyperplasy, and arrest in the process of development hypoplasy.

PHYSIOLOGY

For more advanced study the new edition of Pfeffer's Physiology of Plants, as well as Jost's Lectures on Plant-Physiology, both of which are translated into English, and the lists of literature contained in them may be consulted.

On separate aspects of Physiology further information will be found in Ad. Mayer, Agrikulturchemie, 5th edition, Heidelberg, 1901, 1902; Haberlandt, Physiologische Pflanzenanatomie, 2nd edition, Leipzig, 1896; Schimper, Plant-Geography, English edition, Oxford, 1903; Höber, Physikal. Chemie d. zelle u. d. Gewebe, Leipzig, 1902; Czapek, Biochemie d. Pflanzen, Jena, 1905.

(1) **Mez, Flora, xciv. 1905, includes literature.**

The law of van 't Hoff, that the rapidity of a chemical reaction is about doubled by raising the temperature 10°, has also been verified for some physiological phenomena. In the organism, however, there are usually anti-reactions which conceal the primary dependence on the temperature, and give rise to the well-known cardinal points with an optimum which is soon reached. Literature in review by Jost, Biol. Zentralbl. xxvi. 1906.

According to Becquerel (Compt. rend. 140, 1905) dry seeds can withstand without injury temperatures of −190°.

On the geographical distribution of plants see Schimper, Plant-Geography, Eng. ed. 1903. Drude, Handb. der Pfl.-Geogr. 1890. Grisebach, Veget. d. Erde, 1872. Engler, Versuch einer Entwicklungsgesch. d. Pflanzenwelt, Leipzig, 1879 and 1882. Solms-Laubach, Leitende Gesichtspunkte d. allg. Pfl.-Geogr. Leipzig, 1905. Ihne, Phänolog. Karte des Frühlingseinzugs in Mitteleuropa.; Peterm. Mitt. 1905, Heft 5. Höck, Ankömmlinge in d. Pflanzenwelt; Beihefte Bot. Zentralbl. II. xviii. 1904.

(2) Andrews, Jahrb. f. wiss. Bot. xxxviii. 1902. Mottier, Annals of Bot. xiii. 1899. Miehe, Flora, vol. lxxxviii. 1901. Früh, Abbildung d. vorherrschenden Winde durch die Pflanzenwelt, Zürich, 1901-2. (3) Pfeffer, Osmotische Untersuchungen, 1877. De Vries, Jahrb. f. wiss. Bot., vol. xiv.; *ibid.* vol. xvi. Botan. Ztg. vol. xlvi. 1888, and vol. xlvii. 1889. (4) Schwendener, Das mech. Prinzip im anatom. Bau der Monokotylen, 1879. (5) Haberlandt, Physiolog. Pflanzenanatomie, 2nd edition, 1896, p. 134 ff. Tschirch, Flora, xciv. 1905. (6) Ambronn, Jahrb. für wiss. Bot. vol. xii. 1879. (7) F. Schwarz, Phys. Unters. üb. Dickenwachst. u. Holzqual. von Pinus silv., Berlin, 1899. Hartig, Holzuntersuchungen, Berlin, 1901. Wiedersheim, *ibid.* xxxviii. 1903. O. Melville Ball, Jahrb. f. wiss. Bot. xxxix. 1903. Vöchting, Nachr. Kgl. Ges. d. Wissensch. Göttingen M. N. Kl. 1902, Heft 5. Ursprung, Ber. dtsch. Bot. Ges. 1901. Sonntag, Jahrb. für wiss. Bot. xxxix. 1903. Hartig, Holzuntersuch., Berlin, 1901, p. 53. Wildt, Inaug.-Diss., Bonn, 1906. (8) Noll, Thiel's Landw. Jahrb. vol. xxix. 1900, p. 361. (9) Nägeli, Denkschr., schweiz. Naturf.-Ges. vol. xxxiii. 1893. Moore and Kellermann, U.S. Dep. of Agricult. 1905. Masayasu Kanda, Journ. Coll. of Sc. Tokyo, vol. xix. (Review, Sorauer, Ztschr. f. Pfl.-Krankh. 15.) (10) Winogradsky, Ann. de l'Inst. Pasteur, 1890, 1891. Arch. d. sc. biol. Inst. imp. d. Méd. expér. à St.-Pétersb. 1892. Zentralbl. f. Bakteriol. 1896. Stutzer, Mitteil. d. Landw. Instituts d. Univ., Breslau, 1898. Behrens, Arbt. d. Bakt. im Boden, etc. Arb. deutsch. Landw. Gesell. 1901, Heft 64. Löhnis, Zentralbl. f. Bakt. II. xiii. 1904. Benecke and Keutner, Ber. dtsch. Bot. Ges. xxi. 1903. Keutner, Wiss. Meeresuntersuch. vol. viii. Kiel, 1904. (11) Literature in: A. Fischer, Vorles. über Bakterien, 2nd edition, Jena, 1903, and in Hiltner in Lafars, Handb. d. technischen Mykologie, 2nd edition, vol. iii. Benecke and Keutner, Ber. dtsch. Bot. Ges. 1903, xxi. Reinke, Ber. dtsch. Bot. Ges. xxi. 1903, and xxii. 1904. (12) Saida, Ber. dtsch. Bot. Ges. 1901, xx. J. Kühn, Fühlings Landw. Ztg. 1901, p. 1. Warmboldt, Unters. über d. Biol. stickstoffbind. Bakterien. Inaug.-Diss., Göttingen, 1905. Haselhoff and Bredemann, Landwirtschaftliche Jahrbücher, xxxv. 1906. (13) Benecke, Bot. Ztg. 1903, i.

p. 79. v. PORTHEIM, Sitzber. Wien. Akad. vol. cx. I. (14) v. D. CRONE, Sitzber. Niederrh. Ges. f. Natur- u. Heilkunde, Bonn, 1902, and Inaug.-Diss., Bonn, 1904. (15) RADLKOFER, Ber. dtsch. Bot. Ges. xxii. 1904. ROTHERT (Alumin.), Bot. Ztg. i. xciv. 1906. GÖSSL (Mangan.), Beiheft Bot. Zentralbl. xviii. I. 1905. (16) WIEGMANN and POLSTORFF, Über die anorgan. Bestandteile d. Pflanzen, 1842. Cf. v. LIPPMANN, in Chemikerzeitung, 1894. (17) E. WOLFF, Aschenanalysen von land- und forstwirtsch. Produkten 1871 and 1880. (18) N. WILLE, Festschrift f. Schwendener, 1899, p. 321. (19) PFEFFER, Landw. Jahrb. 1876. Osmotische Untersuchungen, 1877. Zur Kenntnis d. Plasmahaut u. d. Vakuolen, Abh. math.-phys. Klasse Kgl. Sächs. Ges. d. Wiss. 1890. Über Aufnahme u. Ausgabe ungelöster Körper; *ibid.* and Pfl.-Phys., 2nd edition, vol. i. chap. iv. (20) NATHANSOHN, Ber. dtsch. Bot. Ges. 1901, p. 509. PULLST, Jahrb. f. wiss. Bot. xxxvii. 1902. (21) G. SCHRÖDER, Über die Austrocknungsfähigkeit d. Pflanzen, Inaug.-Diss., Leipzig, 1886. AL. BRAUN, Betrachtungen über die Verjüngung i. d. Natur, 1850, p. 213. KURZWELLY, Jahrb. f. wiss. Bot. xxxviii. 1903. FRITZ MÜLLER, Kosmos, vol. xiii. 1883, and Prometheus, vol. ix. Heft 1. (22) THIEL, Landw. Zentralbl. 1870. NOBBE, Versuchsstat. 1875. POND, U.S. Fish. commiss. Rep. for 1903, Washington, 1905. BÜSGEN, Flora, xcv. 1905. Ergbd. RACIBORSKI, Bull. Acad. d. sc., Cracovie, 1905. KUNZE, Jahrb. f. wiss. Bot. xlii. 1906. (23) HALES, Ess. of veg. statics, 1727. G. KRAUS, Flora, 1882, and Forschung. a. d. Gebiet d. Agrikult.-Phys. 1887. CHAMBERLAIN, Rech. s. l. sève ascend., Bull. du. Lab. d. Bot. gén. de l'Univ. de Genève, vol. ii. 1897. PITRA, Jahrb. f. wiss. Bot. 1877. (24) FIGDOR, Sitzber. Wien. Akad. d. Wiss. cvii. 1898. MOLISCH, Bot. Ztg. i. 1902. (25) STRASBURGER, Leitungsbahnen, Jena, 1891, p. 537. v. HÖHNEL, Über d. negat. Druck der Gefässluft, Inaug.-Diss. Strassb. 1876, and Jahrb. wiss. Bot. 1879. NOLL, Sitzber. niederrh. Ges., Bonn, 1897. STRASBURGER (Luftverdünnung), *l.c.* p. 712. DIXON and JOLY, Ann. of Bot. 1895. Report of a Discussion on the ascent of water, British Assoc. Liverpool, Sept. 1896. (26) ASKENASY, Verhandl. naturhist.-med. Verein Heidelberg, 1895 and 1896. STEINBRINCK, Ber. dtsch. Bot. Ges. 1902. DIXON, Scient. Proc. Roy. Soc. Dublin, vol. x. 1903. COPELAND, Bot. Gaz. xxiv. 1902. SACHS, Arb. Botan. Institut Würzburg, vol. ii. and Ges. Abhandl. i. p. 23. KAMERLING, Bot. Zentralbl. 1898. URSPRUNG, Beihefte z. Bot. Zentralblatt, xviii. 1904, and xix. 1906, Jahrb. f. wiss. Bot. xlii. 1906. STEINBRINCK, Flora, xciv. 1905, and Jahrb. f. wiss. Bot. xlii. 1906. (27) ASKENASY, Verh. nat. med. Ver., Heidelberg, 1896. STRASBURGER, Leitungsbahnen. (28) SCHWENDENER, Monatsber. Kgl. Akad. d. Wiss., Berlin, Juli 1881, and Sitzber. d. Akad. d. Wiss., Berlin, 1889. LEITGEB, Mittlg. d. Bot. Inst., Graz, 1886. STAHL, Bot. Ztg. 1894. KOHL, Bot. Beiblatt d. Leopoldina, 1895. FR. DARWIN, Phil. Transact. Roy. Soc., London, vol. cxc. ser. B. p. 531. COPELAND, Ann. of Bot. lxii. 1902. BURGERSTEIN, Die Transpiration der Pflanzen, Jena, 1904, includes literature. (29) v. HÖHNEL, Mittlg. a. d. forstl. Versuchswesen Österreichs, 1879, and Forsch. a. d. Gebiet d. Agrikult.-Phys. 1881. HABERLANDT, Wiss.-prakt. Unters. a. d. Gebiete des Pflanzenbaues, 1877. BÜSGEN, Bau u. Leben der Waldbäume, 1897, p. 168. (30) Cf. STAHL and DARWIN in 27, BUSCALIONI and POLACCI, Atti del Istit. bot. dell' Univ. de Pavia, vii. 1902. (31) TREUB, Ann. Jard. Bot., Buitenzorg, 1889. KRAUS, Flora, vol. lxxxi. 1895. KOORDERS, Ann. Jard. Bot., Buitenzorg, 1897. MOLISCH, Ber. dtsch. Bot. Ges. xxi. 1903. (32) GOEBEL, Flora, lxxvii. 1897. PERCY GROOM, Ann. of Bot. 1897. HABERLANDT, Jahrb. f. wiss. Bot. 1897, p. 27. (34) NOLL, Flora, 1893. (35) SCHIMPER, Die epiphytische Veget. Amerikas, 1888, and Indo-malayische Strandflora, 1891. SCHIMPER, Pflanzengeographie, Jena, 1898. GOEBEL, Pflanzenbiolog. Schilderungen I. KIHLMANN,

Pflanzenbiolog. Untersuchungen in Russisch-Lappland, 1891. (36) Cf. PFEFFER, Pfl.-Physiol. 2nd edition, vol. i. § 60. BEYERINCK, Progr. de la soc. holl. des sciences à Harlem, 1904. The results of KOHL, Ber. dtsch. Bot. Ges. 1897, Heft 2, that the ratio is 5 : 4, is due to an error in calculation. (37) ENGELMANN, Bot. Ztg. 1884, 1887, 1888, Verh. Akad. Amst. 1894. REINKE, Bot. Ztg. 1886. ENGELMANN, Arch. f. Anat. u. Physiol. 1902. GAIDUKOW, Abh. Berl. Akad. d. Wiss., Anhang 1902. PANTANELLI, Jahrb. f. wiss. Bot. xxxix. 1903. REINKE, Lehrb. f. wiss. Bot. x. 1876. MOLISCH, Bot. Ztg. lxiii. 1905, i. Abt. TSWETT, Bot. Ztg. lxiii. 1905. TSWETT, Ber. dtsch. bot. Ges. xxiv. 1906. KOHL, Ber. dtsch. bot. Ges. xxiv. 1906. STAHL, Naturw. Wochenschr. 1905. No. 45. (38) DETLEFSEN, Arb. Bot. Inst., Würzburg, 1888, vol. iii. HOR. BROWN, Address to the Chem. Sect. Brit. Assoc. for advance of Science, 1900. REINKE (Ergrünen), Sitzber. Preuss. Akad., Berlin, 1893. LÖB, Landwirtsch. Jahrb. xxxv. 1906, Heft 4.

ENGELMANN and GAIDUKOW found that *Oscillaria sancta* assumed a red colour in green light, a green colour in red light, a blue-green colour in yellow light, and a brownish-yellow colour in blue light. They term this property complementary chromatic adaptation, and see in it a confirmation of the action of pigments as sensibilisators.

(39) The criticism in an English review that the intermediate products are not evident from this equation, rests on a misunderstanding of the character of chemical equations. According to SCHLOESING, Compt. rend. vol. cxxxi. more O is liberated than CO_2 decomposed.

(40) KREUSLER, Landw. Jahrb. 1885. GODLEWSKI, Arb. Bot. Inst. Würzburg, vol. i. H. BROWN, cf. under No. 32 BROWN and ESCOMBE, FARMER and CHANDLER, Proc. Roy. Soc. 1902, lxx. BROWN and ESCOMBE, Proc. Roy. Soc. lxxvi. 1905. MATTHAEI, Phil. Trans. Roy. Soc. Lond., cxcvii. 1904. BLACKMAN, Ann. of Bot. xix. 1905. BLACKMAN and MATTHAEI, Proc. Roy. Soc. Lond., lxxvi. 1905. DEMOUSSY, Compt. rend. cxxxix. 1904.

According to a recent result CO can be utilised when the percentage present is considerable (?).

(41) H. BROWN and ESCOMBE, Static Diffusion of Gases and Liquids in relation to the assimilation of Carbon and translocation in Plants, Phil. Trans. Roy. Soc. ser. B. 193, 223, 1900. (42) F. HOFMEISTER, Die chemische Organisation der Zelle. Braunschweig, F. Vieweg u. Sohn, 1901. (Naturw. Rundschau xvi. 1901.) G. BREDIG, Anorgan. Fermente usw., Leipzig, W. Engelmann, 1901. S. BENECKE in 12). (43) SCHULZE, Zeitschr. f. physiol. Chemie, vol. xxiv., Landw. Jahrb. vol. xxvii.

According to STEPHAN 1 mgr. NaCl requires about 1 year to penetrate from a 10% solution for a distance of 1 metre into water, cane sugar would require 2½ years, and albumen fully 14 years. The greater rapidity of osmotic movements in the organism therefore presupposes acceleratory influences.

(44) W. OSTWALD. Über Katalyse. Naturw. Rundschau, xvi. Jahrg. 1901. HOFMEISTER, *ibid.* p. 581 ff. G. BREDIG, *l.c.* CZAPEK, Antifermente, Ber. dtsch. Bot. Ges. xxi. 1903. (45) A. FISCHER, Jahrb. f. wiss. Bot. xxii. 1890. MÜLLER-THURGAU, Landw. Jahrb. xi. 1882.

According to NIKELEWSKI, Beihefte Bot. Zentralbl. xix. 1905, the transformations of starch, sugar, and oil in trees not only depend on external influences, but in large part on the internal periodicity of the vital processes.

(46) WEEVERS (Glucosides), Jahrb. f. wiss. Bot. xxxix. 1903. BEYERINCK, On the formation of Indigo etc. Verh. Kon. Akad. v. Wetenschap. te Amsterdam, 31, Sept. 1899. On Indigo-Fermentation, *ibid.* 31, März 1900. MARCHLEWSKI,

Bull. Acad. d. Sc. d. Crocovie, 1902. W. Busse, Mitt. a. d. Labor. d. Kais. Gesdhts.-Amts, 1900. (47) Treub, (Pangium) Ann. Jard. Bot., Buitenzorg, 1895. Guignard, Bull. d. Séances Soc. nat. d'Agricult. de France, 1906. Journ. of the Board of Agricult. 1906. Mallèvre, Journ. de la Soc. centrale d'Agricult. de Belgique, 1906. Mitt. d. deutsch. Landw. Gesellsch. 1906, No. 21. Kniep (Latex), Flora, xciv. 1905. Further Pfeffer, Pfl.-Phys.•2. Aufl., vol. i. § 78–91. (48) Solms-Laubach, Bot. Ztg. 1874. Also in Engler-Prantl, Rafflesiaceae, 1889, iii. 1. Poklo (Neottia), Flora, xcv. 1905, Ergbd. (49) L. Koch, Jahrb. f. wiss. Bot. 1888, and Ber. dtsch. Bot. Ges. 1887. Heinricher, Jahrb. f. wiss. Bot. 1897, 1898, 1901. v. Wettstein, *ibid.* and Österr. Bot. Ztschr. 1897. Johow, Jahrb. f. wiss. Bot. 1889. P. Groom, Ann. of Bot. 1895, and Linn. Journ. Bot. vol. xxxi. E. Laurent, Compt. rend. t. cxxxiii. 1901. Heinricher, Jahrb. f. wiss. Bot. xxxiv. 1901; *ibid.* xxxvii. 1902. (50) Percy Groom, Ann. of Bot. ix. 1905, Linn. Soc. Journ. xxxi. Janse, Ann. Jard. Bot., Buitenzorg, 1896. Frank, Lehrbuch, vol. i. p. 259. Kamienski, Bot. Ztg. 1881. Pfeffer, Landw. Jahrb. 1877. Treub, Ann. Jard. Bot., Buitenzorg, 1886. Sarauw, Bot. Tidsskrift, vol. xviii. p. 127. E. Stahl, Jahrb. f. wiss. Bot. 1900, vol. xxxiv. p. 539. W. Magnus, *ibid.* vol. xxxv. p. 205. MacDougal and Lloyd, Bull. of the New York Bot. Garden, vol. i. No. 5, 1900, p. 419. Möller, Zeitschr. für Forst- und Jagdwesen, 1902. Möller, Ber. deutsch. bot. Ges. xxiv. 1906. Shibata, Jahrb. f. wiss. Bot. xxxvii. 1902. Hiltner, Naturw. Ztschr. f. Land- u. Forstwirtsch. i. 1903. (51) Hellriegel and Wilfarth, Untersuch. über die Stickstoffnahrung der Gramineen u. Leguminosen, 1888. Other literature most recently collected by Hiltner in Lafars, Handb. d. Techn. Mykologie, 2nd edition, 3rd vol. (2. Liefg.). (52) Nikitinsky, Jahrb. f. wiss. Bot. xl. 1904. Abel and Buttenberg, Zeitschr. f. Hygiene, vol. xxxii. p. 449. Galli-Valerio and Strygowski, Pharm. Post, 1900, Heft 45. (53) Sachs, Bot. Ztg. 1853. de Bary, Die Erscheinung der Symbiose, Strassburg, 1879. Schwendener, Nägelis Beiträge z. wiss. Bot. 1861, 1862, 1868, and Flora, 1872. Über Algentypen der Flechtenkonidien, 1869. Bornet, Rech. sur les gonidies des lich., Ann. sc. nat. 5e sér. tome xvii. Stahl, Beitr. zur Entwickl.-Gesch. d. Flechten, 1877 and 1878. Reess, Monatsber. Berlin. Akad. der Wissensch. 1871. Strasburger, Deutsch. Rundschau, 1891. Artari, Bull. d. sc. nat. de Moscou, 1899, No. 1. Cf. also the literature for Cryptogams (83–91). (54) Strasburger, Über Azolla, 1873. (55) Brandt, Arch. f. Anat. u. Phys. (Phys. Abt.) 1882. Belt, Naturalist in Nicaragua, London, 1874. Schimper, Wechselbeziehungen zw. Pflanzen u. Ameisen, 1888. Warburg, Biol. Zentralbl. 1892. A. Möller, Pilzgärten einiger südam. Ameisen, 1893. Fairchild and Cook, Science, 1898. Holtermann, Festschrift für Schwendener, 1899. Raciborski, Flora, 1900, p. 87. Warming, Videnssk. Meddel. Nat. Foren i. Kobhvn, 1893. Morteo, Malpighia, vol. xviii. 1904. Rettig, Beihefte Bot. Zentralbl. xvii. 1904. Ule, Englers, Jahrb. xxxvii. 1905, and Flora xciv. 1905. Also (Ant-garden), in Karsten and Schenck, "Vegetationsbilder." 4 Reihe, Heft 1, 1906, and Naturw. Wochenschr. N. F. v. 1906. (56) Clautriau, Mém. publ. par l'acad. roy. de Belgique, t. lix. 1900. (57) Ad. Mayer, Compt. rend. 1900. i. p. 1389. Griffon, Compt. rend. 1900, vol. cxxx. Puriewitsch, Physiol. Unters. üb. Pflanzenatmung, Jahrb. f. wiss. Bot. 1900, vol. xxxv. p. 573.

Ingenhauss already held correct views on the distribution of the respiratory process. (Wiesner, Jan Ingenhouss, Wien, 1905.)

(58) Ad. Mayer, Poggend. Ann. vol. cxlii. 1871. Wortmann, Arb. Bot. Inst., Würzburg, 1880. Wilson, Flora, 1882. Pfeffer, Unters. Bot. Inst., Tübingen,

1885. E. Godlewski sen. and Polzeniusz, Bull. Krak. Lit. Akad., April 1, 1901, Kostytschew, Ber. dtsch. Bot. Ges. xx. 1902. Ewart, Journ. Linn. Soc. Bot. xxxiii. 123. (59) Winogradsky, Bot. Ztg. 1887, 1888. Molisch, Die Pflanze in ihrer Bez. z. Eisen, 1892. Pfeffer, Energetik, 1892. Pfeffer, Physiology of Plants, vol. i. ch. ix. Buchner and Rapp, Zeitschr. f. Biol. vol. xxxvii. 1898. Nathansohn, Mitt. d. zool. Station Neapel, xv. 1902. Hinze, Ber. dtsch. Bot. Ges. xxi. 1903. Schorler, Zentralbl. f. Bakt. II. xii. 1904. (60) The œcological significance of the products of fermentation, and especially of alcoholic fermentation, was made clear by Lindner, Wochenschr. f. Brauerei, xvii. 1900, Wortmann, Weinbau u. Weinhandel, 1902, and Wortmann, Die wissensch. Grundlagen der Weinbereitung u. Kellerwirtsch., Berlin, 1905, ch. ix. Cf. also A. Fischer, Vorl. über Bakterien, 2nd edition, Jena, 1903. (61) Reinke, Wissenschaftl. Meeresunters. Neue Folge, vol. iii. Heft 2, p. 39. Molisch, Bot. Ztg., i. Abt. 1903, Heft, 1. Molisch, Leuchtende Pflanzen, Jena, 1904, and Sitzber. k. Akad. Wiss. Wien, M. N. Kl. vol. xiii. 1904, and vol. xiv. 1905. O. Zacharias, Biol. Zentralbl. xxv. 1905.

According to the investigations of Tappeiner and others, fluorescent substances in the presence of light are oxygen-activators; they are thus able to initiate profound chemical processes. (Index of literature in Schroeder, Bot. Ztg. 1905, ii. Abt.)

Noll, Arb. Bot. Inst. Würzburg. iii. 1888. Molisch, Sitzber. Wien. Akad. der Wiss. cx. 1901. (62) Stahl, Ber. dtsch. Bot. Ges. 1885. K. Rosenvinge, Rev. génér. de Bot. vol. i. 1889, Nos. 2–5. H. Winkler, Ber. dtsch. Bot. Ges. vol. xviii. 1900, p. 297. Peirce and Randolph, Bot. Gaz. xl. 1905.

The formative processes at the growing points may, as "plastic movements," be in a sense compared with the changes of form of naked protoplasts (amoebae), and thus be reckoned among phenomena of movement. (Noll, Biol. Zentralbl. xxiii. 1903.)

(63) Müller-Thurgau, Landw. Jahrb. d. Schweiz, 1898, vol. xii. Fritz Müller, Kosmos, 6. Jahrg. 1882, Heft 5. Swingle, Science, 1899, N. S. vol. x. Noll (Parthenokarpie d. Gurke), Sitzber. Niederrh. Ges. f. Natur- u. Heilkunde, Bonn, 1902.

Solacolu, G. R. Acad. sc., Paris, 1900, cxli., describes parthenocarpic fruits also for *Brassica oleracea acephala*, *Lonicera caprifol.*, *Papaver Rhoeas*, *Paeonia*, *Lilium*, *Lunaria*, and *Rhododendron*.

Tschermak, Ber. dtsch. Bot. Ges. xx. 1902. Regeneration: Göbel, Biol. Zentralblatt xxii. 1902, and Flora, xcv. 1905, Ergänzungsband. Flora, xciii. 1904, xcii. 1903. Th. H. Morgan, M'Callum, Bot. Gaz. xl. 1906. Němec, Regeneration, Berlin, 1905; Regeneration, New York, 1901. (64) Vöchting, Über Organbildungen im Pflanzenreich, 1878. Vöchting, Bot. Ztg., i. Abt. lxiv. 1906. Sachs, Arb. Bot. Inst. Würzburg, vol. ii. 1880 and 1882. Noll, *ibid.* 1888. Sachs, Lectures, No. 31. Göbel, Organogr. vol. ii. pp. 226 ff. Klebs, Willkürl. Entwicklungsänderungen, Jena, 1903. Janse, Jahrb. f. wiss. Bot. xlii. 1906. Tobler, *ibid.* 1906. Miehe, Ber. dtsch. Bot. Ges. xxiii. 1905. (65) Harting, Linnaea, 1847. Sachs, Jahrb. f. wiss. Bot. 1860, and Arb. Bot. Inst. Würzburg, vol. i. 1874. Strehl, Unters. über das Längenwachstum, etc., 1874. Askenasy, Verh. naturhist.-med. Ver. Heidelberg, 1878. Kraus, Ann. Jard. Bot. Buitenzorg, xii. 1895. (66) Nägeli, Stärkekörner, 1858. Butschli, Uber d. Bau quellbarer Körper, etc. Verh. K. Ges. d. Wiss. Göttingen, 1896. Pfeffer, Phys. of Plants, vol. i. § 12. (67) Askenasy, Verh. nat.-med. Ver. Heidelberg, 1878. Pfitzer, *ibid.* 1882. Janse, Maandbl. v. Natuurwetensch. 1887. F. Benecke, Ber. dstch. Bot. Ges. 1893. G. Kraus, Ann. Jard. Bot. Buitenzorg, vol. xii. p. 196. A.

Möller, Schimper's Bot. Mitt. aus den Tropen, vii. 1895. (68) Popovici, Bot. Zentralbl. 1900, vol. lxxxi. pp. 33, 87. Miyake (Taraxacum), Beihefte Bot. Zentralbl. xvi. 1904. (69) Pfeffer, Phys. of Plants, vol. ii. ch. vi. Sachs, Arb. Bot. Inst. Würzburg, 1871. N. Ono, Journ. Coll. Sc. Imp. Univ. Tokyo, 1900. xiii. 1. (70) Pedersen, Arb. Bot. Inst. Würzburg, 1874. v. Liebenberg, Bot. Zentralbl. 1884. Pammer, Osterr.-ungar. Ztschr. f. Zuckerind. u. Landw. 1892. Schindler, Die Lehre vom Pflanzenbau. Wien, C. Fromme, 1896. Gen. Part, p. 79. (71) Stahl, Jen. Zeitschr. f. Naturw. xvi. 1883. Vöchting, Jahrb. f. wiss. Bot. xxv. 1893. Göbel, Biolog. Zentralbl. xxiv. 1904, and Sitzber. Bayr. Akad. d. Wiss. xxvi. 1896. Flora, xcv. 1905, Ergbd. Nordhausen, Ber. dtsch. Bot. Ges. xxi. 1903. Kornicke, Ber. dtsch. Bot. Ges. xxii. 1904, and xxiii. 1905. (72) Karsten, Bot. Ztg. 1888. Askenasy, *ibid.* 1870. H. Schenck, Biol. d. Wassergewächse, 1886. Göbel, Pflanzenbiol. Schilderungen ii. Abschn. vi. M'Callum, Bot. Gaz. xxxiv. 1902. Pfeffer, Über Druck- und Arbeitsleistung durch wachsende Pflanzen. Abh. K. Sächs. Ges. d. Wiss. 1893, vol. xx. Kny, Ber. dtsch. Bot. Ges. 1896, Jahrb. f. wiss. Bot. vol. xxxvii. 1900, p. 55. Němec, Flora, 1899. Ball, Jahrb. f. wiss. Bot. xxxix. 1903. Noll, Sitzber. Niederrh. Ges. f. Natur- u. Heilkunde, 1901. Townsend, Annals of Bot. xi. 1897. (73) Pfeffer, Phys. of Plants, vol. ii. ch. ix. R. Semon, Biol. Zentralbl. xxv. 1905. Volkens, Gartenflora, lii. 1903. Raciborski, Ann. Buitenzg. ii. Ser. ii. 1. Ursprung, Bot. Ztg. i. Abt. 1901. W. Johannsen, Das Ätherverfahren beim Frühtreiben, etc., Jena, Gustav Fischer, 2nd edition, 1906. B. Schmidt, Ruheperiode der Kartoffelknollen. Ber. dtsch. Bot. Gesellsch. 1901, p. 76. (74) Strasburger, Deutsche Rundschau, 1898, p. 402, 1899, p. 90. Figure of Taxodium mexicanum by Tule in Prometheus xiv. 1903, p. 648. (75) Hofmeister, Die Lehre v. d. Pflanzenzelle, Leipzig, 1867. Engelmann, Bot. Ztg. 1881, 1883, 1886, 1887. Pfeffer, Untersuch. Bot. Inst. Tübingen, vol. ii. Rothert, Flora, 1901, vol. lxxxviii. p. 406. v. Dungern, Ztschr. f. allg. Physiol. i. 1. Buller, Ann. of Bot. 1900. Experiments with drops of mercury: S. Bernstein, Pflüger's Archiv, vol. lxxx. Shibata (Chemotaxis), Jahrb. f. wiss. Bot. lxi. 1905. Topo- and Phobotaxis, recognised by Pfeffer, Phys. of Plants, iii. 215. (76) Kühne, Ztschr. f. Biol. vol. xxxv. N. F. xvii. 1897. Ritter, Flora, 1899, vol. lxxxvi. p. 326. Josing, Jahrb. f. wiss. Bot. xxxvi. 1901. Kritzschmar, Jahrb. f. wiss. Bot. xxxix. 1903. Ewart, On the Physics and Physiology of Protopl. Streaming, Oxford, 1903. (77) Arthur, Annals of Bot. vol. xi. 1897. Ternetz, Jahrb. f. wiss. Bot. vol. xxxv. Heft 2. Senn, Vortrag, lxxxvii. Jahrvers. Schweiz. naturf. Ges. Winterthur, 1904. Küster, Ber. deutsch. bot. Ges. xxiii. 1905. Küster, Ber. deutsch. bot. Ges. xxiv. 1906. Schröter, Flora, cxv. 1905, Ergbd. (78) Steinbrinck in Ber. dtsch. Bot. Ges. 1897, 1898, 1899, 1901, and Schwendener-Festschr. 1899. Kamerling, Flora, 1898. Bot. Zentralblatt, 1898. Schwendener, Sitzber. Preuss. Akad. 1899, and Schrodt, Ber. dtsch. Bot. Ges. 1901, p. 483. Ursprung, Jahrb. f. wiss. Bot. xxxviii. 1903. Schwendener, Sitzber. Preuss. Akad. Berlin, 1902. Steinbrinck, Ber. dtsch. Bot. Ges. xx. 1902, and xxi. 1903, see also under 26. Göbel, Flora, lxxxviii. vol. 1901. (79) Sachs, Arb. Bot. Inst., Wurzburg, 1878, vol. ii. Vochting, Psychroklinie, Ber. dtsch. Bot. Ges. 1898, p. 37. Lidforss, Jahrb. f. wiss. Bot. xxxviii. 1902. Neljubow, Beihefte Bot. Zentralbl. x. 1901. Richter, Ber. dtsch. Bot. Ges. xxi. 1903, p. 180. Singer, Ber. dtsch. Bot. Ges. xxi. 1903. (80) Czapek, Jahrb. f. wiss. Bot. 1895, and *ibid.* 1900, p. 313. F. Darwin, Ann. of Bot. xiii. 1899, p. 567. Němec, Die Reizleitung und die reizleit, Gewebe, Jena, Gust. Fischer, 1901. Němec, Jahrb. f. wiss. Bot. 1901. Haberlandt, Jahrb. f. wiss. Bot. xxxvii. 1902, and xxxviii. 1903. Noll, Ber. dtsch. Bot. Ges. 1902. Miehe, Jahrb.

f. wiss. Bot. xxxvii. 1902. Massart, Mém. cour. Acad. Belg., Bruxelles, 1902. Darwin, Statolith Theory, Proc. Roy. Soc. lxxi. 1903. H. Schroeder, Beihefte Bot. Zentralbl. xvi. 1904. Tischler, Flora, xciv. 1905. Piccard, Jahrb. f. wiss. Bot. xl. 1904. Haberlandt, Verh. Ges. dtsch. Naturf. u. Ärzte. Allgem. Tl. 1904. Haberlandt, Lichtsinnesorgane der Laubblätter, Leipzig, 1905. Statoliths Jahrb. f. wiss. Bot. xlii. 1906. Conduction of Stimuli: Fitting, in Ergebnisse der Physiologie by Asher and Spiro (includes list of literature).

The tonic significance of the growing point for perception and the ensuing reaction has been termed by Miehe (Jahrb. f. wiss. Bot. xxxvii. 1902) tonic prevalence.

(81) Noll, Flora, 1893. Steyer, Reizkrümm. bei Phycomyces., Inaug.-Diss., Leipzig, 1902. Molisch, Sitzber. Wien. Akad., M.-N. Kl. cxi. 1. (82) Stahl, Über sog. Kompasspflanzen, Jen. Ztschr. f. Naturw. 1881. Arthur, Bull. Purdue Univ. 1894. (83) Oltmanns, Flora, 1892, 1897. Elfving, Finska Vet.-Soc. Förhandl. xliii. 1901. O. Richter, Sitzber. K. Akad. d. Wiss. Wien., M.-N., Kl. vol. cv. 1906. (84) Knight in Ostwald's Klassikern, No. 62, 1895. Noll, Het. Ind., Leipzig, 1892. Czapek, Jahrb. f. wiss. Bot. 1898, vol. xxxii. p. 224. Noll. *ibid.* 1900, vol. xxxiv. p. 465. Němec, Ber. dtsch. Bot. Ges. 1900, p. 241, and Jahrb. f. wiss. Bot. 1901, p. 2. Haberlandt, Ber. dtsch. Bot. Ges. 1900, p. 261. (85) Baranetzky, Flora, 1901, Ergbd. lxxxix. p. 138. Noll, Arb. Bot. Inst., Würzburg, vol. iii. ix. and xiii. Schwendener and Krabbe, Abh. Kgl. Pr. Akad. d. Wiss., Berlin, 1892. Noll, Flora, 1892. Meissner, Bot. Zentralbl. 1894. Fitting, Jahrb. f. wiss. Bot. xli. 1905. Luxburg, *ibid.* Czapek, *ibid.* xlii. 1906. (86) Baranetzky, Mém. Acad. imp. St. Pétersbourg, ii. Ser. T. xxxi. 1883. Schwendener, Monatsber. Berlin. Akad. Dez. 1881. Wortmann, Bot. Ztg. 1886. Sachs, Lectures, No. 38. H. Schenck, Beitr. z. Biol. der Lianen, 1892. Noll, Heterog. Induktion, 1892, p. 46. Kolkwitz, Ber. dtsch. Bot. Ges. 1895. (87) Sachs, *l.c.* Lect. 38. Noll, Heterog. Ind. S. 48. Noll, Sitzber. Niederrh. Ges. f. Nat.- u. Heilk., 8. Juli 1901. (88) Hartig, Holzuntersuchungen. Altes u. Neues, Berlin, 1901. Seedlings of Cucurbitaceae: Noll, Landw. Jahrb. xxx. Ezgbd. 1901. Load-curvature: Wiesner, Sitsber. d. K. Akad. d. Wiss. Wien, M.-N. Klasse, vol. cxi. 1902. (89) Wortmann, Bot. Ztg. 1881. M. Miyoshi, Bot. Ztg. 1894, and Flora, 1894. Molisch, Sitzber. Wien. Akad. 1893. Stahl, Bot. Zeitg. 1880. Wortmann, Bot. Ztg. 1883, 1885. J. af Klerker, Ofversigt Kongl. Vetensk. Acad. Förh. 1891. Brunchorst, Bot. Zentralbl. 1885, vol. xxiii. Hegler, Verh. Ges. Deutsch. Naturf. u. Ärzte, 1891. Newcombe, Science 1901. Juel, Jahrb. f. wiss. Bot. 1900, vol. xxxiv. p. 507. Berg, Lunds Univ. Arsskrift 35, No. 6. Sammet, Jahrb. f. wiss. Bot. xli. 1905. Galvanotropism: Gassner, Bot. Ztg. 1906, i. Abt. Ewart and Bayliss, Proc. Roy. Soc. lxxvii. 1905. Schellenberg, Flora, xcvi. 1906. (90) Sachs, Arb. Bot. Inst. Würzburg, vol. ii. 1882 (1879). Noll, Het. Ind., Leipzig, 1892, pp. 12, 35. Czapek, Jahrb. f. wiss. Bot. 1898, vol. xxxii. p. 188. Noll, Jahrb. f. wiss. Bot. 1900, vol. xxxiv. p. 459. Baranetzky, Flora, 1901. Ergänz.-Bd. 89. (91) Noll, Flora, 1893. (92) Schwendener, Monatsber. Berl. Akad. Dec. 1881. O. Müller, Ranken d. Cucurbitac. Inaug. Diss., Breslau, 1886. (Cohn's Beitr., vol. iv. Heft 2.) (93) Pfeffer, Unters. Bot. Inst. Tübingen, vol. i. Haberlandt, Sinnesorgane, Leipzig, 1901. Fitting, Jahrb. f. wiss. Bot. xxxviii. 1903. (94) Nordhausen, Jahrb. f. wiss. Bot. 1899, vol. xxxiv. p. 236. Peirce, Ann. of Bot. 1894. (95) Pfeffer, Pflanzenphys. Unters., Leipzig, 1871, and Periodische Bewegungen, etc. 1875. Oltmanns, Bot. Ztg. 1895. Jost, Jahrb. f. wiss. Bot. 1898. Wiedersheim, Jahrb. f. wiss. Bot. xl. 1904. Burgerstein, Jahrber. Erzherzog Rainer-Gymnasium, Wien, 1902. Farmer, New Phytologist, London, vol. i.

Chemonasty: WÄCHTER, Ber. deutsch. bot. Ges. xxiii. 1905. (96) See under 95. JOST and SCHWENDENER, Sitzber. K. Preuss. Akad. d. Wiss. 1897 and 1898. MOLISCH, Ber. dtsch. Bot. Ges. xxii. 1904. (97) STAHL, Bot. Ztg. 1897, p. 71. A. FISCHER, Bot. Ztg. 1890. NOLL, Het. Ind. 1892, p. 9. (98) SACHS, Flora, 1863. KABSCH, Bot. Ztg. 1861, 1862. DARWIN, Bewegungsvermögen, 1881, p. 271. PFEFFER, Pfl.-Physiol. 1881, vol. ii. § 59. SACHS, Lectures, No. 34. (99) HABERLANDT, Das reizleitende Gewebesystem der Sinnpflanze, Leipzig, 1890. MACDOUGAL, Botan. Gazette, 1896. vol. xxii. p. 293. FITTING, Jahrb. f. wiss. Bot. xxxix. 1903. (100) SACHS, Flora, xlvi. 1863. A. FISCHER, Jahrb. f. wiss. Bot. xxvii. 1894. (101) PFEFFER, Physiol. Untersuchungen, 1873. (102) JOST, Bot. Ztg. 1897. MÖBIUS, Biol. Zentralbl. 1891. (103) KLEBS, Biol. Zentralbl. 1889, and Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen, 1896, and Jahrb. wiss. Bot. 1898 (Sporodinia). OLTMANNS, Morphol. u. Biologie der Algen, vol. ii. Allgem. Teil, Jena, 1905. (104) BEYERINCK, Verh. Kon. Akad. v. Wetensch., Amsterdam, 1900, p. 352. KLEBS, Jahrb. f. wiss. Bot. xlii. 1906. (105) v. KÖLLIKER, Ztschr. f. wiss. Zoologie, vol. xiv. 1864, p. 174. H. DE VRIES, Die Mutationstheorie. Vers. und Beobacht. über die Entstehung d. Arten im Pflanzenreich, Leipzig, Veit and Co. 1901 and 1903. Die Mutationen u. d. Mutationsperioden. Vortr. a. d. Naturf.-Vers. Hamburg, Leipzig, 1901. Ber. dtsch. Bot. Ges. xxi. 1903. MOLL, Biol. Zentralbl. vol. xxi. 1901, vol. xxii. 1902 (review). KORSCHINSKY, Flora, 1901, Ergbd. lxxxix. p. 240. CORRENS, Archiv f. Rassen- und Ges.-Biol. i. 1904. SOLMS-LAUBACH, Bot. Ztg. lviii. 1900. JOHANNSEN, see under 119, DE VRIES, Species and Varieties, their origin by Mutation. Lectures edited by MACDOUGAL, Chicago and London, 1905. LOTSY, Vorles. über Deszendenztheorie, Jena, 1905.

According to GRAND EURY (Compt. rend. cxlii. 1908) *Stigmaria ficoides* can be traced in absolutely constant forms throughout geological strata which must have required fully a million years for their deposition.

According to ARNOLD ENGLER, characters of the Firs of mountains and plains are inherited for a long period by their descendants. The same appears to hold for the Larch and the Alpine Maple. (Mitt. Schweiz. Zentralanst. f. forstl. Versuchsw. viii. Heft 2, 1905.)

[According to a personal communication Herr Oberförster MELSHEIMER found the form of Shepherd's Purse which SOLMS-LAUBACH named *Capsella Heegeri*, in the year 1882. It occurred in hundreds of individuals on the Dattenberg at Linz on the Rhine. Specimens still preserved by H. MELSHEIMER are undoubtedly identical with *Capsella Heegeri*, Solms.]

(106) A. ERNST (Polyembryony), Flora, lxxxviii. 1901 (includes literature to 1901). LOTSY, Ann. Buitenzorg, 2. Ser. i. FARMER, MOORE and DIGBY, Proc. Roy. Soc. vol. lxxi. 1903. Polyembryonie v. *Euphorbia dulcis*: HEGELMAIER, Ber. dtsch. Bot. Ges. xxi. 1903. DE BARY, Bot. Ztg. KUPPER, Flora, xcvi. 1906. KÜSTER, Vermehrung und Sexualität, Vortrag-Samml.: Aus Natur u. Geisteswelt, Leipzig, 1906. (107) See literature for Phanerogams (11a). WINKLER Ber. dtsch. Bot. Ges. xxii. 1905. BITTER, Abh. Nat. Ver. Bremen, xviii. 1904. (108) LOEB, Amer. Journ. of Phys. 1900, Vol. iv. p. 178. WINKLER, Nachr. d. Kgl. Ges. d. Wiss., Göttingen, 1900, Heft 2. NATHANSOHN, Ber. deutsch. Bot. Ges. 1900, p. 99. WINKLER, Jahrb. f. wiss. Bot. vol. xxxvi. 1901, p. 753. E. STRASBURGER, Bot. Ztg. 1901, ii. Abt. p. 353. JICKELI, Unvollkommenh. des Stoffwechsels, etc., Berlin, Friedl. Sohn, 1902, and *ibid.* Vortrag Naturw. Vereins, Siebenbürgen, 1902. KIRCHNER, "Parthenogenesis" in higher plants. Ber. dtsch. bot. Ges. xxii. 1903. (108a) DIGBY, Proc. Roy. Soc. lxxvi. 1905.

From the point of view of comparative morphology it is also possible to speak of apospory in those Hieracia in which an embryo does not develop in the embryo-sac (macrospore) but (according to OSTENFELD and ROSENBERG) in a cell of the nucellus which displaces and replaces the embryo-sac.

(109) HÄCKER, Jen. Zeitschr. f. Naturw. xxxvii. 1902, N. F. 30, also as separate from G. Fischer. DE VRIES, Befruchtung u. Bastardierung, Leipzig, Veit und Comp. 1903.

In the Uredineae in which the formation of the æcidium starts with a cell fusion the nuclei remain distinct until the formation of the teleutospores; the cells are thus bi-nucleate (BLACKMAN, Ann. of Bot. xviii. 1904. Christman, Bot. Gaz. xxxix. 1905).

(110) STEVENS, Bot. Gaz. 1899, vol. xxviii. pp. 129, 225. STEVENS, Bot. Gaz. xxxii. 1901.

A transition to the uninucleate condition of the oospore and to a normal fertilisation is found in Alb. Tragopogonis.

WINKLER (Merogony), Jahrb. f. wiss. Bot. xxxvi. 1901. (111) SOLMS-LAUBACH, Bot. Ztg. 1900, ii. 374. STRASBURGER, Bot. Ztg. 1900, ii. 307, 1901, ii. 353. WINKLER, Jahrb. f. wiss. Bot. xxxvi. 1901, 753. (112) F. KÖRNICKE in Handbuch des Getreidebaues i. by KÖRNICKE and WERNER, Berlin, 1885, and Sitzber. Niederrhein. Ges. f. Natur- u. Heilkunde, Bonn, 1872. NAWASCHIN, Ber. dtsch. Bot. Ges. 1900, vol. xviii. p. 224. GUIGNARD, Compt. rend. vol. cxxviii. 1899, p. 869, and Ann. sc. nat. Bot., 8. sér. vol. xi. 1900, p. 365, Journ. de Bot. xv. 1901. DE VRIES, Rev. gén. de Bot. vol. xii. 1900, p. 129. CORRENS, Ber. deutsch. Bot. Ges. 1899, p. 410. STRASBURGER, Bot. Ztg. ii. Abt. 1900, p. 293. CORRENS. Bastarde zwischen Maisrassen, etc., Bibl. Bot. 1901, Heft 53. (113) CORRENS, Ber. dtsch. Bot. Ges. 1900, vol. xviii. p. 422. (114) H. SCHENCK, Die Biologie der Wassergewächse, 1886. (115) CHR. K. SPRENGEL, Das entdeckte Geheimnis d. Natur im Bau u. in der Befruchtung d. Blumen, 1793. (Also in Ostwald's Klassikern, Nos. 48-51.) DARWIN, Works. HERM. MÜLLER, The Fertilisation of Flowers. F. HILDEBRANDT, Die Geschlechtsverteilung bei den Pflanzen, etc. 1867.

MACLEOD, Bot. Jaarb. Dodon. Gent, 1890, gives 688, KNUTH in Handb. d. Blütenbiol. to April 1, 1898, 2871 papers on this subject.

FR. JOHOW, Sitzber. K. Pr. Akad. d. Wiss. 1898. VOLKENS, in Schwendener-Festschrift, 1899. F. JOHOW, Zur Bestäubungsbiologie Chil. Blüten, ii. Verh. d. wiss. Ver. Santiago, vol. iv. p. 345. Valpar. 1901. Includes a list of Ornithophilous flowers. E. WERTH, Verh. d. bot. Ver. d. Pr., Brandenburg, 1900, vol. xlii. p. 222. BURCK (Chiropterophilous) flowers, Ann. Buitenzg. 1892. HART, Bull. of Misc. Inform. 1897. MARLOTH, Ber. deutsch. Bot. Ges. xix. 1901. DETTO, Flora, xciv. 1905. ANDREAE, Beiheft Bot. Zentralbl. xv. 1903. GILTAY, Jahrb. f. wiss. Bot. xl. 1904.

Flying insects appear to be mainly attracted by colours, and creeping insects by scents, but no sharp distinction can be made on these lines.

(116) HILDEBRANDT, Ber. dtsch. Bot. Ges. 1896. Cleistogamy: GÖBEL, Flora, xcv. 1905. Ergbd. HACKEL, Österr. Bot. Ztschr. lvi. 1906.

The pollen of chasmogamous flowers also, according to Göbel, may germinate within the pollen sacs in a damp hot-house.

Monœcious and Diœcious Mucorineae: BLAKESLEE, Proc. of the Amer. Acad. of Arts and Sciences, xl. 4, 1904. Heterostyly: ERRERA, Rec. de l'Inst. bot. de Bruxelles, 1905. (117) KOELREUTER, Vorläuf. Nachr. v. einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen, 1761, 1763, 1764, 1766.

Gärtner, Versuche und Beobachtungen über Bastarderzeugung der Pflanzen, 1849. Mendel, Flora. 1901, Ergbd. lxxxix. p. 364. Correns, Bot. Ztg. 1900, Sp. 229. Hildebrandt, Bot. Zentralbl. vol. lxxix. 1899, pp. 9, 36. Solms-Laubach, Bot. Ztg. 1902, ii. Abt. Sp. 10. Tischler, Jahrb. für wiss. Bot. xlii. 1906. (118) Strasburger, Jahrb. für wiss. Bot. vol. xvii. 1886. (119) Correns, Sammelref. Bot. Ztg. 1903, ii. 113. Includes reviews of literature. de Vries, Compt. rend. cxxxvi. 1903. de Vries, Befruchtung u. Bastardierung, Leipzig, Veit and Comp. 1903. Review Naturw. Rundschau, 1902, p. 640, and Naturw. Rundschau, 1903, 214. Tschermak, Ztschr. f. d. Landw. Versuchsw. Österr. 1901, 1902, and 1904. Johannsen, Erblichkeit in Populationen, etc., Jena, G. Fischer, 1903. Correns, Ber. dtsch. Bot. Ges. xx. 1903, and xxi. 1904. Correns, Mendel's Briefe an C. Nägeli, Abh. Math.-phys. Klasse Sächs. Ges. d. Wiss. xxix. 1905. Tschermak, Wien. Landw. Zeitung, 1905. Tschermak, Arch. f. Rassen- and Gesellsch.-Biologie, 2. Lotsy, Vorles. über Deszendenztheorie, Jena, 1905. Correns, Vererb. Gesetze, Vortrag, Berlin, 1905. Strasburger, Stoffliche Grundl. der Vererbung, Jena, 1905. Strasburger, Allen, Miyake, and Overton, Histol. Beiträge zur Vererbungsfrage, Jahrb. für wiss. Bot. xlii. 1906. Morgan, Germ Cells of Mendel pure? Biol. Zentralbl. lxxxvi. 1906.

Annual and biennial races also follow Mendel's laws (Correns, Ber. deutsch. bot. Ges. xxii. 1904).

(120) Zea canina: Contribut. from the Bot. Laborat. Univ. of Pennsylvania, ii. 1901. Cyt. Adami: Darwin, Ges. Werke, übers. v. Carus, 1878, vol. iii. Laubert, Bot. Zentralblatt, Beihefte, x. 1901. Tischler, Ber. deutsch. Bot. Ges. xxi. 1903. Crataegus: Köhne, Gartenflora, l. 1901. Noll, Sitzber. niederrhein. Ges. f. Natur- und Heilkunde, Bonn, 1905. Strasburger, Jahrb. f. wiss. Bot. xlii. 1906. (121) Dingler, Ber. dtsch. Bot. Ges. 1887, and Flora, 1887, and Beweg. der pflanzlichen Flugorgane, 1889. Ridley, Ann. of Bot. xix. 1905 (seed). Falck, Beitr. z. Biol. d. Pfl., vol. ix. 1904 (spores). (122) Schimper, Indo-malayische Strandflora, 1891, pp. 158 ff. Schimper, Pflanzengeographie, Jena, G. Fischer, 1900. (123) Burgerstein, Wien. Gartenztg. 1901. Duggar, Bot. Gaz. xxxi. 1901. Schulz, Flora, xi. 1901. Hard seed-coat: Hiltner, Arb. Biol. Abt. Kaiserl. Ges.-Amt Land- und Forstwirtschaft, 1901, and Naturw. Zeitschr. für Land- und Forstwirtschaft, 1906 (influence of concentrated H_2SO_4 on seeds of Conifers). Schoene, Flora, xcv. 1905. Ergänzungsband.

According to the researches of Neger (Naturwiss. Zeitschr. für Land- und Forstwirtschaft, vol. ii.) the spores of Bulgaria when in water soon lose their power of germinating, but this returns on their drying in the vicinity of decaying parts of plants.

Heinricher, Beihefte Bot. Zentralbl. xiii. 1902. Inga: Borzi, Atti d. Reale Acad. d. Lincei Rendiconti, 1903, ser. v. vol. xii. (124) Germination: Peter, Nachr. Götting. Ges. d. Wiss. 1893. Schindler, Die Lehre vom Pflanzenbau auf physiol. Grundlage, 1896, p. 36 ff. Hiltner, Arb. Biol. Abt. Kais. Ges.-Amt Land- u. Forstwirtschaft, iii. 1902. (125) Klebs, Unters. Bot. Inst. Tübingen, vol. i. p. 536 ff. (126) Pfitzer, Ber. deutsch. Bot. Ges. 1885. (127) Cucurbita: cf. 88. de Vries, Landw. Jahrbücher, 1880. Rimbach, Die kontraktilen Wurzeln. Fünfstücks, Beitr. z. wiss. Bot. vol. ii. 1897, and Ber. dtsch. Bot. Ges. 1899, vol. xvii. p. 18.

CRYPTOGAMS

(1) Klebs, Die Beding. der Fortpflanz. bei niederen Algen und Pilzen, 1896, and Jahrb. f. wiss. Botanik, xxxii.-xxxiv.; further Willkürl. Entwicklgsänd. bei Pflanzen, 1903. (2) A. Fischer, Vorlesungen über Bakterien, 1897, 2nd edition, 1903. Flügge, Die Mikroorganismen, 1896. Migula, System der Bakterien, 1897-1900, and Nat. Pflfam. I^1. Migula, A. de Bary's Vorlesungen über Bakterien, 3rd edition, 1900. Kolle and Wassermann, Handb. der pathogen. Mikroorganismen, 1904. A. Meyer, Flora, 1899, p. 428. (3) Sorauer, Lindau, Reh, Handbuch der Pflanzenkrankheiten, 1906. (4) Thaxter, Bot. Gaz. xiv. 1892, p. 389, xxiii. 1897, p. 395, and xxxvii. 1904, p. 405. Quehl, Ctrbl. für Bakt., Parasitenkunde, etc., xvi. 1896, p. 9. (5) Kirchner, in Nat. Pflfam. I^1. A. Fischer, Unters. über den Bau der Cyanophyceen und Bakterien, 1897; also Bot. Zeitg. 1905, p. 51. Zacharias, Abhand. aus dem Geb. der Naturw., Hamburg, 1900, and Jahrb. d. Hamburger wiss. Anstalten, xxi. 1903. Hegler, Jahrb. f. wiss. Bot. xxxvi. 1901, p. 229. Massart, Recueil de l'inst. bot. de Bruxelles, v. 1902. Brand, Ber. deutsch. bot. Ges. 1901, p. 152, 1905, p. 62, and Beihefte bot. Zentralbl. xv. 1903, p. 31. Kohl, Organisation und Physiol. d. Cyanophyceenzelle, Jena, 1903, and Beihefte bot. Zentralbl. 1905, xviii. p. 1. Fritsch, Beihefte bot. Zentralbl. 1905, xviii. p. 194. Olive, Beihefte bot. Zentralbl. 1905, xviii. p. 9. Philipps. Contrib. bot. Lab. Pennsylvania, ii. 1904, p. 237. (6) Oltmanns, Morphologie und Biologie der Algen, i. 1904. (7) Senn, in Nat. Pflfam. I^1. (8) Zumstein, Jahrb. f. wiss. Bot. xxxiv. 1900, p. 149. (9) Schröter, in Nat. Pflfam. I^1. De Bary, Comparative Morph. and Biol. of the Fungi, Mycetozoa and Bacteria. Zopf, Die Pilztiere, 1885. Lister, A Monograph of the Mycetozoa, 1894. Harper, Bot. Gaz. xxx. 1900, p. 217. Jahn, Ber. deutsch. bot. Ges. 1904, p. 84, 1905, p. 489. (10) Woronin, Jahrb. f. wiss. Bot. xi. 1878, p. 548. Nawaschin, Flora, 1899, p. 404. Prowazek, Arb. kais. Gesundheitsamt, xxii. 1905, p. 396. (11) Schütt, in Nat. Pflfam. I^1, and Die Peridin. der Planktonexpedition, 1895. Schilling, Flora, 1891, p. 220. (12) Schütt, Das Pflanzenleben der Hochsee, 1893. Gran, Das Plankton des norwegischen Nordmeeres, 1902. (13) Schilling, Ber. deutsch. bot. Ges. 1891, p. 199. (14) Zederbauer, Ber. deutsch. bot. Ges. 1904, p. 1. (15) De Bary, Unters. über die Konjugaten, 1858. Ralfs, The British Desmidieae, 1848. Wille, in Nat. Pflfam. I^2. W. West and G. S. West, A Monograph of the Brit. Desmid. i. 1004. Lütkemüller, Beitr. z. Biol. d. Pflanz. viii. 1902, p. 347. Klebahn, Jahrb. f. wiss. Bot. xxii. 1891, p. 415. (16) Chmielewsky, Arb. d. Gesellsch. d. Naturf. d. Charkower Universität, xxv. 1890. (17) Smith, Synopsis of the Brit. Diatom. 1853-56. Schmidt, Atlas der Diatomeenkunde, Leipzig, 1874-77. Van Heurck, Synopsis des Diat. 1880-85, and Traité des Diat., Anvers, 1899. Dippel, Diatomeen der Rhein-Mainebene, 1905. Pfitzer, in Bot. Abh. von Hanstein I^2, 1871. Klebahn, Jahrb. f. wiss. Bot. xxix. 1896, p. 595. Karsten, Flora, 1896, p. 286, 1897, pp. 33, 203, 1900, p. 253, and Die Diatomeen der Kieler Bucht, 1899. Schütt, in Nat. Pflfam. i., and Jahrb. f. wiss. Bot. 1899-1900. O. Müller, Ber. deutsch. bot. Ges. 1898-1903. (18) Gran, Die Diat. der arkt. Meere, Fauna arctica, iii. 1904. Karsten, Ber. deutsch. bot. Ges. 1904, p. 544, and Wiss. Ergebn. der d. Tiefseeexped. ii. 1905. (19) Benecke, Jahrb. f. wiss. Bot. xxxv. 1900, p. 535. Karsten, Flora, Ergzb. 1901, p. 404. (20) Kützing, Tabulae phycologicae. (21) Wille, in Nat. Pflfam. I^2. (22) Wille, Algolog. Notizen ix.-xiv., Christiania, 1903. Schmidle, Ber. deutsch. bot. Ges. 1903, p. 346. (23) Goroschankin,

Flora, 1905, p. 420. (24) Klein, Jahrb. f. wiss. Bot. xx. 1889, p. 133, and Ber. nat. Ges. Freiburg, v. 1890. Overton, Bot. Zentralbl. xxxix. 1889, p. 65. A. Meyer, Bot. Ztg. 1896, p. 187. (25) Beyerinck, Bot. Ztg. 1890, p. 720. (26) Grintzesco, Rev. génér. de bot. xv. 1903, p. 5. (27) Senn, Bot. Ztg. 1899, p. 39. (28) Askenasy, Ber. deutsch. bot. Ges. 1888, p. 129. (29) Klebs, Bot. Ztg. 1891, p. 789, and Flora, 1890, p. 351. Timberlake, Transact. Wiscons. Acad. xiii. and Annals of Bot. xv. 1901, p. 619. (30) Dodel, Jahrb. f. wiss. Bot. x. 1876, p. 417. Klebs, Beding. der Fortpfl. bei Algen und Pilzen, 1896. (31) Pringsheim, Jahrb. f. wiss. Bot. i. 1858, p. 1. Juranyi, *ibid.* ix. 1873-74, p. 1. Klebahn, *ibid.* xxiv. 1892, p. 235. (32) Pringsheim, *ibid.* ii. 1860, p. 1. Oltmanns, Flora, 1898, p. 1. Allen, Ber. d. bot. Gesellsch. 1905, p. 285. (33) De Bary and Strasburger, Bot. Ztg. 1877, p. 713. Solms-Laubach, Trans. Linn. Soc. 1895. (34) Reinke, Wiss. Meeresunters., Kiel, 1899. Weber van Bosse, Annales jard. Buitenzorg, xv. 1898, p. 243. Haberlandt, Sitzb. Akad. Wien, cxv. i. 1906, p. 1. (35) Ernst, Beiheft bot. Zentralbl. xiii. 1903, p. 115. Oltmanns, Flora, 1895, p. 388. Davis, Bot. Gazette, xxxviii. 1904, p. 81. (36) Wille, in Nat. Pflfam. I^2. Migula, in Rabenhorst, Krypt. Flora Deutschland, 1890. Götz, Bot. Ztg. 1899, p. 1. Giesenhagen, Flora, 1896, p. 381, and 1898, p. 19. Goebel, Flora, 1902, p. 279. Mottier, Annals of Bot. xviii. 1904, p. 245. (37) Kjellmann, in Nat. Pflfam. I^2. Postels et Ruprecht, Illustr. algarum Oceani pacifici, 1840. Hooker, Flora antarctica, i. 1844. Reinke, Atlas deutscher Meeresalgen, 1889-92. Reinke, Studien zur vgl. Entwicklgsgesch. der Laminarien, Kiel, 1903. (38) Skottsberg, Bot. Notiser, 1903, p. 40. (39) Hansteen, Jahrb. f. wiss. Bot. xxxv. 1900, p. 611. Hunger, *ibid.* xxxviii. 1903, p. 70. (40) Wille, Univers. Festschrift, Christiania, 1897. (41) Berthold, Flora, 1897, p. 398. Oltmanns, Flora, 1897, p. 398 ; 1899, p. 86. Sauvageau, Journ. de botan. 1896. (42) Church, Annals of Bot. xii. 1898, p. 75. Sauvageau, Ann. sc. nat. 8 sér. x. 1899, p. 265. (43) Williams, Annals of Bot. xi. 1897, p. 545, and xviii. 1904, pp. 141, 183 ; xix. 1905, p. 531. (44) Mottier, Annals of Bot. xiv. 1900, p. 163. Strasburger, Bot. Ztg. 1906, ii. p. 3. (45) Thuret and Bornet, Etud. phycolog. 1877. Oltmanns, Bibl. bot., Heft 14. Strasburger, Jahrb. f. wiss. Bot. xxx. 1897, p. 351. Farmer and Williams, Phil. Trans. Roy. Soc. London, vol. cxc. 1898. (46) Schmitz and Hauptfleisch, Nat. Pflfam. I^2. Falkenberg, xxvi. Monogr. Fauna und Flora, Neapel, 1901. Kolkwitz, Wiss. Meeresunters., Kiel, 1900. Wille, Ber. deutsch. bot. Ges., 1894, p. 57, and Nova Acta, lii., 1887, p. 51. Osterhout, Flora, 1900, p. 109. Oltmanns, Bot. Ztg. 1898, p. 99. Hassenkamp, Bot. Ztg. 1902, p. 65. Wolfe, Annals of Bot. xviii. 1904, p. 607. Yamanouchi, Bot. Gazette, xli. 1906, p. 425. (47) Kuckuck, Sitzb. Akad. Berlin, 1894, p. 983. Sturch, Annals of Bot. xiii. 1899, p. 83. (48) De Bary, Comp. Morph. and Biology of the Fungi. (49) Brefeld, Bot. Unters. über Schimmelpilze, Unters. aus dem Gesamtgebiet d. Mykologie, 1872-1905. Von Tavel, Vgl. Morphol. d. Pilze, 1892. (50) Schröter, in Nat. Pflfam. I^1. (51) Cornu, Ann. sc. nat., 1872. Thaxter, Bot. Gaz. 1895. Lagerheim, Bihang till Svensk. Akad. Handl. xxv. Woronin, Mém. de l'Acad. imp. des Sciences de St-Pétersbourg, 1904, 8. sér. vol. xvi. No. 4, p. 1. (52) Trow, Annals of Bot. ix. 1895, p. 609 ; xiii. 1899, p. 130 : xviii. 1904, p. 541. Klebs, Jahrb. f. wiss. Bot. xxxiii. 1899, p. 513. Davis, Bot. Gaz. xxxv. 1903, p. 233. (53) Woronin, Jahrb. f. wiss. Bot. xi. 1978, p. 556. (54) Wager, Annals of Bot. iv. 1889-91, p. 127 ; x. 1896, pp. 89, 295 ; xiv. 1900, p. 263. Berlese, Jahrb. f. wiss. Bot. xxxi. 1898, p. 159. Davis, Bot. Gaz. xxix. 1900, p. 297. Stevens, Bot. Gaz. 1899, xxviii. p. 149 ; 1901, xxxii. p. 77 ; 1902, xxxiv. p. 420, and Ber. deutsch. bot. Ges. 1901, p. 171. Trow, Annals of

Bot. xv. 1901, p. 269. Miyake, Annals of Bot. xv. 1901, p. 653. Rosenberg, Bihang till Svensk. Ak. vol. xxviii. 1903. Ruhland, Jahrb. f. wiss. Bot. xxxix. 1904, p. 135. Rostowzew, Flora, 1903, p. 405. (55) Harper, Annals of Bot. xiii. 1899, p. 467. Gruber, Ber. deutsch. bot. Ges. 1901, p. 51. Dangeard, Compt. rend. acad. Paris, cxlii. 1906, p. 645. (56) Blakeslee, Proceed. Amer. Acad. xl. 1904. (57) Olive, Bot. Gaz. xli. 1906, pp. 192, 229. (58) Eidam, Cohn's Beitr. z. Biol. iv. 1887, p. 181. Raciborski, Flora, 1906, p. 106. Fairchild, Jahrb. f. wiss. Bot. xxx. 1897, p. 285. Woycicki, Flora, 1904, p. 87. (59) Tulasne, Selecta Fungorum Carpologia, 1861-65. Schröter, Lindau, Fischer in Nat. Pflfam. I^1. (60) Harper, Ber. deutsch. bot. Ges. 1895, p. 67, and Jahrb. f. wiss. Bot. xxx. 1897, p. 249 ; also Annals of Bot. xiii. 1899, p. 467 ; xiv. 1900, p. 321. Guilliermond, Revue génér. de bot. xvi. 1904, pp. 49, 130. Claussen, Bot. Ztg. 1905, p. 1. (61) De Bary, Beitr. z. Morphol. und Phys. der Pilze, iii. 1870. Harper, Ber. deutsch. bot. Ges. 1895, p. 475, and Jahrb. f. wiss. Bot. xxix. 1895, p. 655. Neger, Flora, 1901, p. 333, and 1902, p. 221. Salmon, Annals of Bot. xx. 1906, p. 187. Harper, Carnegie Institution of Washington, publ. No. 37, 1902 (Phyllactinia). (62) Harper, Annals of Bot. xiv. 1900, p. 321 (Pyronema). Claussen, Bot. Ztg. 1905, p. 1 (Boudiera). (63) Krombholz, Abb. und Beschreib. der Schwämme, 1831-46. Lenz, Nützl., schädl. und verdächt. Schwämme, 1890. Schlitzberger, Pilzbuch. Michael, Führer für Pilzfreunde. Röll, Unsere essb. Pilze. (64) Goethe, Über den Krebs der Obstbäume, Berlin, 1904. (65) Fischer in Rabenhorst, Krypt. Flora, I^5. (66) Sadebeck, Jahrb. Hamburg. wiss. Anst. 1884, 1890, 1893, and Ber. d. bot. Ges. 1903, p. 539 ; 1904, p. 119. Giesenhagen, Flora, Ergzb. 1895, p. 267, and Bot. Ztg. 1901, p. 115. Ikeno, Flora, 1903, p. 1. (67) Guilliermond, Rev. génér. de bot. 1903, p. 337. Thaxter, Mem. of Amer. Acad., Boston, 1896. Lindau, in Nat. Pflfam. I^1. (70) Dietel, Lindau, Hennings, Fischer in Nat. Pflfam. I^1. (71) Juel, Jahrb. f. wiss. Bot. xxxii. 1898, p. 361. Ruhland, Bot. Ztg. 1901, p. 187. Harper, Bot. Gaz. xxxiii. 1902, p. 1. (72) R. Hartig, Krankh. der Waldbäume, 1874, and Lehrb. der Pflanzenkrankheiten, 1900. (73) Harper, Transact. Wisconsin Acad. 1899, p. 475. (74) Brefeld and Falk, Unt. aus dem Gesammtgeb. d. Mykologie, xiii. 1905. Hecke, Ber. d. Bot. Ges. 1905, p. 248. (75) Numerous papers, Magnus, Klebahn, Sydow, Eriksson, Tischler, E. Fischer, Lagerheim, and others. (76) Blackman, Annals of Bot. xviii. 1904, p. 323. Blackmann and Fraser, *ibid.* xx. 1906, p. 35. Christman, Bot. Gaz. xxxix. 1905, p. 267. (77) Klebahn, Die wirtswechselnden Rostpilze, 1904. (78) Eriksson and Tischler, Svenska Vet. Akad. Handl. 1904, vol. xxxvii., xxxviii. Klebahn, Ber. deutsch. bot. Ges. 1904, p. 255. E. Fischer, Bot. Ztg. 1904, p. 327. Marshall Ward, Annals of Bot. xix. 1905, p. 1. (79) Molisch, Leuchtende Pflanzen, 1904. (80) R. Hartig, Der echte Hausschwamm, 1885 ; 2nd edition by von Tubeuf, 1902. (89) Möller, Pilzgärten südamerik. Ameisen, 1893. Holtermann, Schwendener Festschrift, 1899. Forel, Biolog. Zentralbl. 1905, p. 170. Huber, Biolog. Zentralbl. 1905, p. 606. (82) E. Fischer, Denkschr. Schweiz. nat. Ges. xxxii. and xxxvi. Möller, Brasil. Pilzblumen, 1895. (83) Fünfstück and Zahlbruckner, in Nat. Pflfam. I^1. Reinke, Jahrb. f. wiss. Bot. 1894-96. Schwendener, Algentypen der Flechtengonidien, 1869. Bonnier, Ann. sc. nat. 1889. Bitter, Hedwigia, xl. 1901, p. 171, and Jahrb. f. wiss. Bot. xxxvi. 1901, p. 421. (84) Peirce, Proceed. Calif. Acad. 1899, p. 207, and The Amer. Naturalist, 1900, p. 245. Elenkin, Bull. Jard. Bot. St-Pétersb. iv. 1904. (85) Zopf, Beih. bot. Zentralbl. xiv. 1903, p. 95. (86) Stahl, Häckelfestschrift, 1904, p. 357. (87) Krabbe, Cladonia, 1891. Baur, Bot. Ztg. 1904, p. 21. (88) Stahl, Beitr. z. Entw. d. Flechten, 1877. Baur, Ber. deutsch. bot. Ges. 1898, p. 363, and Flora, 1901,

p. 319; Bot. Ztg. 1904, p. 21. Darbishire, Jahrb. f. wiss. Bot. xxxiv. 1900, p. 329. Lindau, Flora, 1888, p. 451, and Schwendenerfestschrift, 1899. Wolff, Flora, Ergzsb. 1905, p. 31. (89) Möller, Kultur flechtenbild. Ascomyceten, 1887; Bot. Ztg. 1888, p. 421. (90) Glück, Flechtenspermogonien, Habilitationsschr. Heidelberg, 1899. (91) Johow, Jahrb. f. wiss. Bot. xv. 1884, p. 361. Möller, Flora, 1893, p. 254. Poulsen, Vid. Medd. Kopenhagen, 1899. (92) Goebel, Die Muscineen. Schenks Hdb. d. Bot. ii. 1882; Organography, vol. ii.; Flora, 1902. (93) Campbell, The Structure and Development of Mosses and Ferns, 2nd edition, 1905. (94) Goebel, Flora, 1902, p. 279. Davis, Annals of Botany, xvii. 1903, p. 477. Holferty, Bot. Gaz. xxxvii. 1904, p. 106. (95) Ikeno, Beih. bot. Zentralbl. xv. 1903, p. 65 (Marchantia). Johnson, Bot. Gaz. xxxviii. 1904, p. 185 (Monoclea). Lewis, Bot. Gaz. xli. 1906, p. 110 (Riccia). Bolleter, Beih. bot. Zentralbl. xviii.^{1} 1905, p. 327 (Fegatella). (96) Pfeffer, Unters. bot. J. Tübingen, i., ii. Lidfors, Jahrb. f. wiss. Bot. xli. 1904, p. 65. (97) Schiffner, in Nat. Pflfam. I^3. Leitgeb, Unters. über Lebermoose, 1874-82. Goebel, Flora, 1895, p. 1. Andreas, Flora, 1899, p. 161. (98) Garber, Bot. Gaz. xxxvii. 1904, p. 161. Lewis, Bot. Gaz. xli. 1906, p. 110. (99) Kny, Botan. Wandtafeln, viii. 1890. Ikeno, Beih. bot. Zentralbl. xv. 1903. Kamerling, Flora, Ergzb. 1897, p. 1. Bolleter, Beih. bot. Zentralbl. xviii.^{1} 1905, p. 327. (100) Gottsche, Haplomitrium, Nova Acta Acad. Leop. xx. 1843, p. 267. Goebel, Ann. jard. Buitenzorg, ix. 1890, p. 11, and Organography, vol. ii. p. 39. (101) K. Müller, Ruhland, Warnstorf, Brotherus in Nat. Pflfam. I^3. Lorentz, Jahrb. f. wiss. Bot. vi. 1867-68, p. 363. Haberlandt, *ibid.* xvii. 1886, p. 359. Tansley and Chick, Annals of Bot. xv. 1901, p. 1. Correns, Vermehrung der Laubmoose, 1899. Vaupel, Flora, 1903, p. 346. (102) Zederbauer, Östr. bot. Ztschr. 1902. (103) Haberlandt, Jahrb. f. wiss. Bot. xvii. 1880, p. 357. Porsch, Der Spaltöffnungsapparat im Lichte der Phylogenie, 1905, p. 33. (104) Ph. W. Schimper, Torfmoose, 1858. Nawaschin, Flora, 1897, p. 151. (105) Lantzius-Beninga, Der innere Bau der Mooskapsel, 1850. Dihm, Flora, Ergzbd. 1894, p. 286. Goebel, Flora, 1895, p. 459. Steinbrinck, Flora, Ergzbd. 1897, p. 131. (106) Sadebeck, in Nat. Pflfam. I^4. Goebel, Organography II^2. (107) Pfeffer, Unters. bot. Inst. Tübingen, i. p. 363 (Ferns, Selaginella). Shibata, Bot. Mag. Tokyo, xix. 1905, p. 39 (Salvinia); *ibid.* pp. 79, 126 (Equisetum); Ber. d. bot. Ges. 1904, p. 478, and Jahrb. f. wiss. Bot. xli. 1905, p. 561 (Isoëtes). Lidfors, Ber. d. bot. Ges. 1905, p. 314 (Equisetum). (108) Sadebeck, Diels, Bitter in Nat. Pflfam. I^4. Hooker, Synopsis filicum, 1883. Baker, Fern Allies, 1887. Christ, Farnkräuter der Erde, 1897. Bower, Trans. Roy. Soc. 1899, and Proc. Roy. Soc. 1903. (109) Jeffrey, Univers. of Toronto, Biolog. Series, No. 1, 1898 (Botrychium). Bruchmann, Bot. Ztg. 1904, p. 1 (Ophioglossum), and Flora, 1906, p. 203 (Botrychium). Cardiff, Bot. Gaz. xxxix. 1905, p. 340. (110) Lyon, Bot. Gaz. xl. 1905, p. 455 (Botrychium). (111) Steinbrinck, Ber. deutsch. bot. Ges. 1903, p. 217. Ursprung, Jahrb. f. wiss. Bot. xxxviii. 1903, p. 635, and Ber. deutsch. bot. Ges. 1904, p. 73. (112) Strasburger, Jahrb. f. wiss. Bot. vii. 1869-70, p. 390. (113) De Bary, Bot. Ztg. 1878, p. 449. Bower, Trans. Linn. Soc. 1887. Lang, Bot. Zentralbl. lxxiii. 1898, p. 145. Farmer, Moore, Digby, Proc. Roy. Soc. lxxi. 1903. (114) Pringsheim, Jahrb. f. wiss. Bot. iii. 1863, p. 484. Belajeff, Bot. Ztg. 1898, p. 141. (115) Strasburger, Azolla, 1873. (116) Sadebeck, in Nat. Pflfam. I^4. Jeffrey, Mem. of Boston, Soc. of Nat. Hist. v. Ursprung, Jahrb. f. wiss. Bot. xxxviii. p. 655; Ber. deutsch. bot. Ges. 1904, p. 73. Steinbrinck, Ber. deutsch. bot. Ges. 1903, p. 217. (117) Ursprung, Jahrb. f. wiss. Bot. xxxviii. p. 635. (118) Pritzel, in Nat. Pflfam. I^4. Goebel, Bot. Ztg. 1887, p. 161. Treub, Ann. Jard. Buitenzorg, 1884-90.

Bruchmann, Über die Prothallien und Keimpfl. der Lycop. 1898. Lang, Annals of Bot. xiii. 1899, p. 279. (119) Hieronymus, in Nat. Pflfam. I⁴. Pfeffer, in Hansteins Bot. Abh. 1871. Belajeff, Bot. Ztg. 1885, p. 793. Bruchmann, Unters. über Selaginella spinulosa, 1897. Fitting, Bot. Ztg. 1900, p. 107. Goebel, Flora, 1901, p. 207. Lyon, Bot. Gaz. xxxii. 1901, p. 124, and xl. 1905, p. 285. Campbell, Annals of Bot. xvi. 1902, p. 419. Denke, Beiheft z. Bot. Zentralbl. xii. 1902, p. 182. Steinbrinck, Ber. deutsch. bot. Ges. 1902, p. 117. (120) Bruchmann, Flora, 1905, p. 150. Goebel, Flora, 1905, p. 195. (121) Haberlandt, Flora, 1888, p. 291, and Ber. d. bot. Ges. 1905, p. 441. (122) Sadebeck, in Nat. Pflfam. I⁴. Farmer, Annals of Bot. v. 1890-91, p. 37. Scott and Hill, *ibid.* xiv. 1900, p. 413. Smith, Bot. Gaz. xxix. 1900, p. 225. Fitting, Bot. Ztg. 1900, p. 107. Solms-Laubach, *ibid.* 1902, p. 178. Belajeff, *ibid.* 1885, p. 793. Campbell, Mosses and Ferns, p. 536. (123) W. Ph. Schimper, Traité de Paléontologie végétale, Paris, 1866-1874. W. Ph. Schimper and A. Schenk, Palaeophytologie, in Zittel's Handbuch der Pal. 1890. A. Schenk, Die fossilen Pflanzenreste, 1888. B. Renault, Cours de bot. fossile, 1881-85. G. Saporta and Marion, Evolution du règne végétal, 1881 and 1885. Solms-Laubach, Fossil Botany. Potonié, Lehrb. der Pflanzenpaläontologie, 1899. D. H. Scott, Studies in Fossil Botany, 1900. Potonié, Fossile Pteridophyten in Nat. Pflanzenfam. I⁴. R. Zeiller, Eléments de paléobotanique, 1900.

PHANEROGAMS

(1) W. Hofmeister, Vergleich. Untersuch. der Keim., Entfalt. und Fruchtbild. höherer Kryptogamen und der Samenbild. der Koniferen, Leipzig, 1851. (2) E. Strasburger, Angiospermen und Gymnospermen, Jena, 1879. Overton, Reduktion der Chromosomen, Vierteljahrsschr. d. naturf. Ges. Zürich, 1893. Juel, Tetradenteilg., Jahrb. f. wiss. Bot. xxxv. 1900. M. Koernicke, Niederrhein. Ges. 1901. Coulter and Chamberlain, Morphology of Spermatophytes I., New York, 1901. K. Goebel, Organography of Plants. E. Warming, Pollenbildende Phyllome und Caulome, Hanst. bot. Abh. ii. 1873. Strasburger, Bau und Wachstum d. Zellhäute, 1882. Wachstum vegetab. Zellhäute, 1889. Befruchtungsvorgang d. Phanerogamen, Jena, 1884. Wille, Pollenkörner d. Angiospermen, 1886. Belajeff, Pollenschlauch d. Gymnospermen, Ber. d. deutsch. bot. Ges. 1891, 280, and 1893, 196. Strasburger, Verhalten d. Pollens und Befruchtungsvorgänge bei den Gymnospermen, Jena, 1892. G. Klebs, Keimung. Unters. Tübingen, i. 1884. (2a) E. Strasburger, Reduktionsteilung. Sitzgsber. K. Akad. d. W. Berlin, xviii. 1904. Strasburger, Ch. Allen, Kiichi Miyake, I. Bertr. Overton, Histolog. Beitr., Jahrb. f. wiss. Bot. xlii. Leipzig, 1905. Strasburger, Stoffl. Grundlagen der Vererbung, Jena, 1905. O. Rosenberg, Reduktionsteilung. Botan. Notiser, 1905. (3) Eichler, Blütendiagramme i. and ii. Leipzig, 1875, 1878. A. Engler, Prinzipien d. systemat. Anordnung aus Syllabus, 3rd edition, Berlin, 1903. Das Pflanzenreich from 1900. Engler and Prantl, Natürl. Pflanzenfamilien ii. iii. iv. from 1889. Baillon, Histoire des plantes i.-xiii. 1867-94. Berg and Schmidt, Atlas d. offizin. Pflanzen, 1863, and the second edition by A. Meyer and Schumann, 1891-1902. (4) W. Hofmeister, Vgl. Untersuchungen, 1851. Strasburger, Befruchtg. bei d. Koniferen, Jena, 1869. Koniferen und Gnetaceen, Jena, 1872. Angiospermen und Gymnospermen, Jena, 1879. Coulter and Chamberlain, Morph. of Spermatophytes, i. and ii., N.Y. 1901 and 1903. Goebel, Organography of Plants. The literature cited in 3 and 4 includes the

most important and fundamental works dealing with the Phanerogams as a whole; these works will not be referred to below. (5) L. Cl. Richard, Commentatio de Coniferis et Cycadeïs, Stuttgart, 1826. E. Warming, Cycadeerne, K. D. Vidensk. Selsk. Forh. 1877 and 1879. M. Treub, Cycadées, Ann. de Buitenzorg, 2 and 4, 1885. W. H. Lang, Stangeria, Ann. of Botany, xi. 1897, and xiv. 1900. H. J. Webber, Spermatogenesis and Fecundation of Zamia, Washington, 1901, U.S. Dep. of Agricult. S. Ikeno, Cycas revoluta, Jahrb. f. wiss. Bot. xxxii. 1898. H. Graf Solms-Laubach, Stangeria, Bot. Ztg. 1890. G. Kraus, Ann. de Buitenzorg, xiii. 1896. Coulter and Chamberlain, Zamia, Bot. Gaz., March 1903. M. C. Stopes, Cycadeen, Flora, 1904, 435. H. Matte, Cycadacées, Caen, 1904. H. Miyake, Cycas-Spermatozoiden, Ber. der deutschen botan. Gesellsch. 1906. (6) Literature 4, and Sakugoro Hirasé, Ginkgo biloba, Botan. Zentralbl. vol. lxix. No. 2, 1897. Hirase, Journ. of the College of Science, Univ. Imp. Tokio, viii. 1895, and xii. 1898. K. Goebel, Pollenentleerung, Flora, 1902, Ergbd. (7) Literature 4, and Goroschankin, Corpuscula, Bot. Ztg. 1883. J. Sachs, Lehrb. d. Botanik, iv. 1874. L. Celakowsky, Gymnospermen, Abh. kg. bohm. Ges. d. W. 1890. Continued in Engler's Jahrb. 1898. Belajeff, Ber. d. deutsch. bot. Ges. 1891, 280, and 1893, 196. Dixon, Pinus silvestris, Ann. of Bot. 1894. Noll, Abietineen-Zapfen, Sitzgsber. d. niederrh. Ges. 1894. Jäger, Taxus baccata, Flora, 1899. Arnoldi, Gymnospermen, 1, 2, and 5 Bull. de Moscou, 1899, 1900; 3 and 4 Flora, 1900, 6 Russian with resumé in German; J. Wiesner, Rohstoffe des Pflanzenreichs, 2nd edition, 1900. Goebel, Pollenentleerung, Flora, Ergbd. 1902. K. Fujii, Bestäubungstropfen, Ber. d. deutsch. Bot. Ges. 1903. F. W. Oliver, Older Gymnosperms, Ann. of Bot. xvii. 1903. K. Miyake, Abies balsamea, Beih. z. bot. Zentralbl. 1903. Miyake, Picea excelsa, Ann. of Bot. xvii. 1903. A. Lawson, Sequoia, Ann. of Bot. xviii. 1904. Lawson, Cryptomeria, Ann. of Bot. xviii. 1904. E. Strasburger, Taxus, Haeckel-Festschrift, Jena, 1904. Juel, Cupressus, Flora, 1904. W. C. Coker, Taxodium, Bot. Gaz. July and Aug. 1903. Coker, Bot. Gaz. 38, 1904. Margaret Ferguson, Pinus, Proc. Washington Acad. of Sc., vi. Oct. 1904. Coulter and Land, Torreya, Bot. Gaz. xxxix. 1905. E. Stahl, Mexik. Nadelhölzer and L. Klein, Mitteleurop. Waldbäume in "Vegetationsbilder," ii. Reihe, 3 and 5-7, Jena, 1904. (8) Literature 4 and J. D. Hooker, Welwitschia, etc., Trans. Linn. Soc., Lond. xxiv. 1863. F. O. Bower, Welwitschia, Quart. Journ. Micr. Soc. xxi. 1881. Bower, Gnetum Gnemon, *ibid.* xxii. 1882. H. H. W. Pearson, Welwitschia, Phil. Trans. Roy. Soc. Lond., vol. cxcviii. 1906. G. Karsten, Gnetum, Bot. Ztg. 1892. Karsten, Ann. de Buitenzorg, xi. 1893. Karsten, Cohn's Beitr. z. Biol. vi. 1893. Jaccard, Ephedra helvetica, Diss., Zürich, 1893. Lotsy, Gnetum, Ann. de Buitenzorg, xvi. 1899. Lotsy, Parthenogenesis, Flora, 1903. W. J. G. Lund, Bot. Gaz. xxxviii. 1904. (9) W. Ph. Schimper, Traité de Paléontologie végétale, Paris, 1866-74. Schimper and A. Schenk, Palaeophytologie in Zittel's Handbuch der Pal. 1890. A. Schenk, Die fossilen Pflanzenreste, 1888. B. Renault, Cours de bot. fossile 1881-85. G. Saporta and Marion, Evolution du règne végétal, 1881 and 1885. H. Graf zu Solms-Laubach, Fossil Botany. Potonié, Lehrbuch der Pflanzenpaläontologie, 1899; D. H. Scott, Studies in Fossil Botany, 1900; R. Zeiller, Eléments de paléobotanique, 1900. (9a) Potonié, Cycadofilices in Engler, Prantl i. 4, 1901. Scott, Origin of Seed-Bearing Plants, Roy. Inst. of Gr. Britain, 1903. Oliver, Older Gymnosperms, Annals of Bot. xvii. 1903. Oliver and Scott, Phil. Trans. Roy. Soc. Lond. ser. B. cxcvii. 1904. M. C. Stopes, Flora, 1904. M. Benson, Telangium, Ann. Bot. xviii. 1904. C. Grand Eury, Pecopteris, Comptes rendus, 140. E. A. Newell Arber, Lagenostoma, Proc. Roy. Soc., 1905, 76. B.

(10) Literature cited under 3 and 4: also, Payer, Traité d'organogénie de la fleur, 1857. Goebel, Vgl. Entwicklungsgeschichte in Schenk, Handbuch d. Bot. iii. 1, Breslau, 1884. F. Noll, Normale Stellung zygomorpher Blüten, etc. 1885, 1887, Arbeit bot. Inst. Würzburg, iii. H. Voechting, Zygomorphy, Pringsh. Jahrb. xvii. 1886. Voechting, Einfluss des Lichtes, etc., *ibid.* xxv. 1893. Goebel, Gefüllte Blüten, Jahrb. f. wiss. Bot. xvii. 1886. K. Schumann, Blütenmorpholog. Studien, Pringsh. Jahrb. xx. 1889. Warming, Ramification des Phanérog., Vidensk. Selsk. Skr. sér. v. x. 1872. Goebel, Special Morphology, 1882. J. Schniewind-Thies, Septalnektarien, 1897. H. Müller, Befruchtung der Blumen durch Insekten, 1873. P. Knuth, Blütenbiologie, 1 and 2, 1899. C. Detto, Ophrys, Flora, xciv. 287, 1905. (11) Vesque, Sac embryonnaire, Ann. sc. nat. 6 sér. vi. 1878. Strasburger, Befruchtung und Zellteilung, 1878. Strasburger, Befruchtungsvorgang b. d. Phanerogamen, 1884. Strasburger, "Doppelte Befruchtung," Bot. Ztg. ii. Abt. 1900. Strasburger, Befruchtung, Bot. Ztg. ii. Abt. 1901. L. Guignard, Sac embryonnaire, Rev. sc. nat. Montpellier, T. i. 1882. Guignard, Ann. sc. nat. Bot. 6 sér. xii. and xiii. 1882, and 7 sér. xiv. 1891. Guignard, vol. jubil. soc. d. Biologie, 1899. Guignard, Anthérozoides et double fécond., Comptes rend., Paris, 1899. Guignard, Tulipes, Ann. sc. nat. 8 sér. xi. 1900. Guignard, Maize, Najas major; Ranunculaceéae, Journ. de Botan. xv. 1901. Treub, Loranthacées, Ann. d. Buitenzorg, ii. and iii. 1883 and 1885. Treub, Casuarina, Ann. d. Buitenzorg, x. 1891. Treub, Balanophora elongata, Ann. d. Buitenzorg, xv. 1898. S. Nawaschin, Birch, Mém. acad. imp. St-Pétersbourg, vii. sér. 42, No. 12, 1894. Nawaschin, Elm, Bull. acad. imp. St-Pétersbourg, 1898. Nawaschin, Lilium Martagon and Fritillaria tenella, Bull. acad. imp. St-Pétersbourg, 1898. Nawaschin, Corylus Avellana, Bull. 1899. Nawaschin, Dicotyledones, Ber. d. deutsch. bot. Ges. 1900. Westermaier, Antipodal cells, Ber. d. deutsch. bot. Ges. 1898. Benson, Amentiferae, Linn. Soc. London, 1895. Lotsy, Rhopalocnemis phalloides, Ann. d. Buitenzorg, 2 sér. ii. 1900. G. Karsten, Juglandaceae, Flora, 1902. F. E. Lloyd, Rubiaceae, Mem. of the Torrey Bot. Club, viii. 1, 1899, and 2, 1902. Douglas H. Campbell, Peperomia, Ber. d. deutsch. bot. Ges. 1899. Duncan S. Johnson, Peperomia, Bot. Gaz. xxx. 1900. J. Hanstein, Entwicklung des Keimes, Bot. Abhandlung, i. 1, 1870, Bonn. Th. C. Frye, Casuarina, Bot. Gaz. Aug. 1903. Juel, Casuarina, Flora, 1903. P. K. Loetscher, Antipodal Cells, Flora, xciv. 213, 1905. E. Strasburger, Drimys, Flora, Ergzbd. 1905. Ch. H. Shattuck, Ulmus americana, Bot. Gaz. xl. 1905. A. Habermann, Synergidae, Diss., Bonn, 1905. (11a) Sv. Murbeck, Alchemilla, Lunds Univ. Arssk. xxxvi. 1901. H. O. Juel, Antennaria, K. Svensk. Ak. Handl. xxxiii. 1900. Juel, Taraxacum, Bot. Tidsskr. xxv. Kiöbh. 1903, and Arkiv f. Bot. ii. 4, 1904. J. B. Overton, Thalictrum, Bot. Gaz. xxxiii. 1902, and Ber. d. deutsch. Bot. Ges. 1904. C. Raunkiaer and C. H. Ostenfeld, Hieracium, Bot. Tidsskr. 25, 1903. Ostenfeld, Ber. d. bot. Ges. 1904, 376 and 537. Strasburger, Reduction-division, Sitz.-Ber. Ak. W. Berlin, 18, 1904. Strasburger, Apogamy in Eualchemilla, Jahrb. f. wiss. Bot. xli. 1905. G. Bitter, Parthenogenesis, Bryonia, Abh. Nat. Ver. Bremen, 1904. H. Winkler, Parthenogenesis, Ber. deutsch. bot. Ges. xxii. 573, 1905. M. Treub, Elatostema, Ann. de Buitenzorg. 2 sér. 5, 1905. O. H. Juel, Taraxacum and Cichorieae, K. Svensk. Vet. Ak. Handlingar, xxxix. 1905. Sv. Murbeck, Taraxacum and Hieracium, Bot. Notiser, 1904. O. Rosenberg, Hieracium, Ber. d. bot. Ges. vol. xxiv. 1906, 157. (11b) K. Goebel, Cleistogamous flowers, Biolog. Zentralbl. xxiv. 1904. Goebel, Viola, Flora, Ergzbd. 1905. (12) J. Gärtner, De fructibus et seminibus plantarum, i. and ii. Stuttgart, 1789-91. A. P. de Candolle, Pflanzenphysiologie, trans. by Roeper, ii. 212.

F. Hildebrandt, Verbreitungsmittel der Pflanzen, Leipzig, 1873. (13) Literature under 3. Th. Irmisch, Knollen- and Zwiebelgewächse, Berlin, 1850. H. Hallier, Polyphylet. Ursprung der Sympetalen und Apetalen, 1901, Abh. a. d. Geb. der Naturw., Naturw. Verein Hamburg, xvi. E. Sargant, Theory of the Origin of Monocotyledons, etc., Ann. of Bot. xvii., Jan. 1903. Sargant, Bot. Gaz. xxxvii. 1904. K. Fritsch, Stellung der Monokotylen, Beiblatt, 79. Engler's Bot. Jahrb. xxxiv. p. 22, 1905. Goebel, Streptochaeta, Flora, 1895, Ergbd. F. Körnicke, Species and Varieties of Cereals, Handb. d. Getreidebaues by Körnicke and Werner, i. Bonn, 1885. E. Bruns, Embryo of Grasses, Flora, 1892, Ergbd. Schlickum, Biblioth. Botan. xxxv. 1896. A. Nestler, Lolium temulentum, Ber. d. D. bot. Ges. 1898. P. Guerin, Lolium temulentum, Bot. Gaz. 28. A. R. Wallace, Tropical Nature. Alph. de Candolle, Ursprung d. Kulturpflanzen, trans. by E. Goeze, Leipzig, 1884. J. Reinke, Asparageae, Pringsh. Jahrb. xxxi. 1897. Th. Irmisch, Beitr. z. vergl. Morphologie, 1-6, Halle, 1853 - 1879. A. F. W. Schimper, Epiphyt. Veget. Amerikas, Bot. Mitteil. a. d. Tropen. 2, Jena, 1888. C. Mez, Jahrb. f. wiss. vol. xl. 1904. Ch. Darwin, Fertilisation of Orchids. G. Karsten, Monocotyledonous Trees, in "Vegetationsbilder," 1. Reihe, 6, Jena, 1903. R. von Wettstein, Sokotra, in "Vegetationsbilder," 3. Reihe, Heft 5, Jena, 1905. (13a) Buchenau in Engler and Prantl, ii. 1, 228. (13b) H. Glück, Alismaceen, Jena, 1905. (14) Literature under 3, also: J. Lubbock, Contrib. to the Knowl. of Seedlings, vols. i. and ii. 1892. H. Hallier, Vorläufiger Entwurf des natürl. (phylogenetischen) Systems der Blütenpflanzen, Bull. d. l'herbier Boissier, 2 sér. iii. 1903. Hallier, Umfang, Gliederung und Verwandtschaft der Familie der Hamamelidaceen, 1903. Hallier, Phylogeny of Engler's Rosales, Parietales, Myrtiflores, etc., Abhandl. d. Naturw. Vereins, Hamburg, 1903. Hallier, Daphniphyllum, Tokio Bot. Mag. xviii. 1904. E. Sargant, Origin of Monocotyledons, Ann. of Bot. xvii. 1903. Sargant, Bot. Gaz. 37, 1904. G. Senn, Hallier's Angiospermensystem, Beih. Bot. Centralbl. xvii. 1904. K. Fritsch, Stellung d. Monokotylen, Beibl. 79, in Engler's Bot. Jahrb. xxxiv. p. 22, 1905. E. Strasburger, Drimys, Flora, Ergbd. 1905, 215. (15) Cf. 3. (15a) Th. Nicoloff, Juglandées, Journ. de Botanique. tt. xxviii.-xxix. 1904-5. (16) H. Graf zu Solms-Laubach, Herkunft, Domestikation und Verbreitung d. gew. Feigenbaumes, Abh. d. Kg. Ges. d. W. Göttingen, 1882. Solms-Laubach, Geschlechtsdifferenz, etc., Bot. Ztg. 1885. Fritz Müller, Caprificus und Feigenbaum, Kosmos, vi. 1882. G. King, Ficus, etc. Linn. Soc. xxiv. G. King, Species of Ficus, Ann. Roy. Bot. Garden, Calcutta, 1887. A. de Candolle, Ursprung d. Kulturpflanzen, trans. by Goeze, 1884. M. Golenkin, Urticaceae and Moraceae, Flora, 1894. O. Warburg, Kautschukpflanzen, Berlin, 1900. E. Ule, Kautschukpfl. der Amazonasexped. Engler's Jahrb. xxxv. 663, 1905. P. Reintgen, Kautschukpflanzen, Beihefte d. Tropenpflanzer. vi. 1905. M. Treub, Ficus hirta, Ann. de Buitenzorg, 2 sér. A. 3, 1902. A. F. W. Schimper, Pflanzen und Ameisen, Bot. Mitteil. a. d. Tropen, i. 1888. E. Ule, Ameisenpflanzen, Engler's Jahrb. xxxvii. 335, 1906. (17) K. Goebel, Verzweigung dorsiventraler Sprosse, Arb. d. Bot. Inst. zu Würzburg, ii. 3, 1880. Goebel, Vgl. Entwicklungsgeschichte, 1884. (17a) Wiesner, Rohstoffe des Pflanzenreichs, 2nd edition, 1900, ii. 305. (18) E. A. Bessey, Russisch-Turkestan, in "Vegetationsbilder," 3. Reihe, Heft 2, Jena, 1905. (18a) H. de Vries, Mutationstheorie, i. 72, and ii. 662, 1901-3. (19) M. Raciborski, Cabombeen und Nymphaeaceen, Flora, 1894. H. L. Lyon, Nelumbo, Minnesota Bot. Stud. ii. 1901. Büsgen, Jensen, Busse in "Vegetationsbilder," 3. Reihe, Heft 3, Jena, 1905. E. Strasburger, Ceratophyllum, Jahrb. f. wiss. Bot. xxxvii. 1902. (20) E.

Janczewski, Anemone, Rev. gén. de Bot. 1892. O. Stapf, Aconites of India. Ann. R. Bot. Garden, Calcutta, x. 1905. (20a) E. Strasburger, Drimys, Flora, 1905, Ergbd. (21) O. Warburg, Muskatnuss, Leipzig, 1897. J. M. Janse, Ann. de Buitenzorg, xvi. 1899. (22) V. Hehn, Kulturpflanzen und Haustiere, 7th edition, 1902. H. Schenck, Mittelmeerbäume in "Vegetationsbilder," 3. Reihe, Heft 4. (23) H. Graf zu Solms-Laubach, Cruciferenstudien, i.-iv. Bot. Ztg. 1900, 1902, 1903, 1905. Hannig, Bot. Ztg. 62, i. Abt. 1904. (24) J. M. Macfarlane, Ann. of Bot. iii. and vii. 1889, 1893. K. Goebel, Pflanzenbiolog. Schilderungen, ii. 1891-93. (24a) Goebel, *ibid.* Wasserpflanzen, 1889. (25) K. Goebel, *ibid.* i. Sukkulenten, 1889. (26) E. de Janczewski, Ribes, 1901, Bull. Acad. Cracovie. G. Tischler, Ribes-Hybriden, Jahrb. f. wiss. Bot. 1906, 42. (27) K. Goebel, Bot. Ztg. 1882. A. de Candolle, Ursprung der Kulturpflanzen, trans. by Goeze, 1884. (28) Th. Belt, Naturalist in Nicaragua, 1888. H. de Vries, Mutationstheorie, i. ii. 1901-3. G. Tischler, Cytisus Adami, Ber. d. deutsch. bot. Ges. 1903. J. Reinke, Leguminosen, i.-vii. Pringsh. Jahrb. xxx. 1896-97. F. Noll, Pfropfbastarde, Sitzber. d. niederrhein. Ges. f. Nat. und Heilk. Bonn, 1905. E. Strasburger, Typ. und Allotyp. Kernteilg. Jahrb. f. wiss. Bot. vol. xlii. 1905, 62. (29) A. de Candolle, Ursprung d. Kulturpflanzen, 1884. V. Hehn, Kulturpflanzen und Haustiere, 7th edition, 1902. (30) Schweinfurth, Erythraea in "Vegetationsbilder," ii. Reihe 8, Tafel 58, Jena, 1905. (31) E. Warming, Pollenbild. Phyllome und Caulome in Hanstein, bot. Abh. ii. 2, 1873. R. Brown, Vermischte Schriften, i. 56, Leipzig, 1825. Rubber plants cf. 16. Jos. Schweiger, Samenentwicklung der Euphorbiaceen, Flora, xciv. 339, 1905. (32) O. Preuss, Expedition nach Zentral- und Südamerika, 1901. (33) J. Wiesner, Rohstoffe des Pflanzenreichs, 2nd edition, 1900. (34) Engelmann, Botanical Works coll. for H. Shaw, edited by W. Trelease and Asa Gray, Cambridge, 1887. Goebel, Pflanzenbiol. Schilderungen, i. Sukkulenten, 1889. G. Heyl, Cacteen, Archiv d. Pharmacie, 1901, includes further literature. G. Karsten and E. Stahl, Mexikan, Cacteen in "Vegetationsbilder," i. Reihe 8, 1903. E. Stahl, Mexikan, Xerophyten, *ibid.* ii. Reihe 4, 1904. (35) H. de Vries, Mutationstheorie, i. and ii. 1901-3. (35a) A. K. Schindler, Halorrhagaceen, Beibl. 77. Engler's Jahrb. xxxiv. 3, 1904. (36) A. F. W. Schimper, Indo-malayische Strandflora, 1891. G. Karsten, Mangroveveget., Bibl. bot. xxii. 1891. Karsten in "Vegetationsbilder," 2. Reihe, Heft 2, Jena, 1904. G. Haberlandt, Mangrovepflanzen, Ann. de Buitenzorg, xii. 1893. Johs. Schmidt in "Vegetationsbilder," 3. Reihe, Heft 7, 1906. (37) H. Graf zu Solms-Laubach, Bau und Entwicklung parasitischer Phanerogamen, Pringsh. Jahrb. vi. 1868. J. Scott, Loranthaceae, Journ. of Agricult. and Horticult. Soc. of India, 1871, and Auszug resp. Übers. (Santalum album) by H. Graf zu Solms-Laubach, Bot. Ztg. 1874, No. 9. (38) Literature under 37, also: M. Treub, Loranthacées, Ann. de Buitenzorg, ii. and iii. 1883 and 1885. L. Jost, Mistel. Bot. Ztg. 1888. T. Johnson, Arceuthobium Oxycedri, Ann. of Botany, ii. F. Johow, Chilen, Blüten, Verh. d. Deutsch. wiss. Ver. Santiago, iv. 1900. L. Klein, Forstbotanik, Lorey's Handb. d. Forstwissenschaft, 2nd edition, 1903. K. Reiche, Phrygilanthus aphyllus, Flora, 1904. (39) H. Graf zu Solms-Laubach, Rafflesiaceen und Hydnoraceen, Bot. Ztg. 1874. Solms-Laubach, Brugmansia Zippelii und Aristolochia Clematitis, Bot. Ztg. 1876. Solms-Laubach, Philostyles Hausknechtii, Bot. Ztg. 1874. Solms-Laubach, Rafflesia, Ann. de Buitenzorg, ix. 1889. Solms-Laubach, Rafflesia und Brugmansia, Ann. de Buitenzorg, suppl. ii. 1897. E. Heinricher, Rafflesiaceae, Denkschr. Akad. Wien. math. naturw. Kl. lxxviii. 1905. (40) M. Treub, Balanophora elongata, Ann. de Buitenzorg, xv. 1898. P. Lotsy, Balanophora globosa, Ann. de

Buitenzorg, xvi. 1899. Lotsy, Rhopalocnemis phalloides, Ann. de Buitenzorg, xvii. 1900. (41) A. Artopoeus, Ericaceen, Flora, 1903. P. Gräbner, Heide Norddeutschlands, Vegetation der Erde, v. 1901. (42) F. Hildebrandt, Monogr. Cyclamen, 1898. K. Goebel, Regeneration, 1902, Biolog. Centralbl. H. Winkler, Regeneration, Ber. d. deutsch. bot. Ges. 1902. (43) A. de Candolle, Ursprung der Kulturpflanzen, trans. by Goeze, 1884. V. Hein, Kulturpflanzen und Haustiere, 7th edition 1902. H. Schenck, Mittelmeerbäume, Jena, 1905, in "Vegetationsbilder," 3. Reihe, Heft 4. P. Knuth, Handbuch der Blütenbiologie, ii. 1899. (44) R. v. Wettstein, Saison-Dimorphismus, Ber. d. deutsch. bot. Ges. xiii. 303. v. Wettstein, Deszendenztheoret. Unters. i., Denkschrift d. k. Akad. d. W. Wien, 1900. (44a) E. Gilg, Strophanthus, Tropenpflanzer, 1902, 11. E. Gilg, H. Thoms. H. Schedel, Strophanthus, Ber. d. Pharmac. Ges. 1904. (45) Kautschukpflanzen, cp. 16. P. Preuss, Expedition nach Zentral- und Südamerika, Berlin, 1901. Kolonial-Wirtschaftl. Komitee, Kunene-Zambesi-Expedition, herausgeg. von O. Warburg, Kolon. Wirtsch. Kom. 1903. (46) M. Treub, Dischidia Rafflesiana, Ann. de Buitenzorg, iii. 1883. (47) G. J. Peirce, Haustoria, Ann. of Botany, 1893. Peirce, Cuscuta, Ann. of Botany, 1894. (48) F. Muth, Symphytum officinale, Flora, Ergbd. 1902. K. Goebel, Boragoid. Flora, Ergbd. 1902. (49) Koorders, Tectona grandis, Natuurk. Tydskr. v. Ned. Ind. 1893. (50) M. Treub, Avicennia officinalis, Ann. de Buitenzorg, iii. 1883. (51) A. F. W. Schimper, Pflanzen und Ameisen, Bot. Mitteil. a. d. Tropen, i. 1888. (52) H. Müller, Befruchtung d. Blumen durch Insekten, 1873. (53) E. Heinricher, Lathraea, Ber. d. k. Akad. d. W. Wien, 1892, and Ber. d. deutsch. bot. Ges. 1893. Heinricher, Halbschmarotzer, i.-iv. Jahrb. f. wiss. Bot. 1897, 1898, 1901, 1902. R. v. Wettstein, Euphrasia, Öst. bot. Ztschr. 1894, 1895. v. Wettstein, Monogr. Euphrasia, 1896. Sterneck, Monogr. Alectorolophus, 1901. J. Hoffmann, Odontites, Öst. bot. Ztschr. 1897. K. Goebel, Tozzia und Lathraea, Flora, 1897. G. Haberlandt, Hydathoden, Jahrb. f. wiss. Bot. 1897. (54) Hielscher, Streptocarpus, Cohn's Beiträge, iii. 1878. (55) K. Goebel, Morphol. und biolog. Studien, v. Ann. de Buitenzorg, ix. Goebel, Pflanzenbiol. Schilderungen, ii. 116 : Lentibularieae, 1891. Goebel, Flora, 1904, 98. (56) H. Müller, Blumen und Insekten. P. Knuth, Blütenbiologie. (57) M. Treub, Plantes grimpantes, Ann. de Buitenzorg, iii. 1883. (58) M. Treub, Myrmecodia echinata, Ann. de Buitenzorg, iii. 1883, and vii. 1888. K. Schumann, Ameisenpflanzen, Jahrb. f. wiss. Bot. xix. 1888. (59) K. Goebel, Campanula rotundifolia, Flora, 1896, and Flora, Ergbd. 1905. Herm. Müller, Blumen und Insekten. P. Knuth, Blütenbiologie. R. Schultz, Monogr. d. G. Phyteuma, 1904. (60) F. Noll, Cucurbitaceen, Landw. Jahrb. xxx. Ergbd. P. 1901. F. Noll, Parthenocarpie, Sitzber. d. niederrh. Ges. f. Natur- und Heilk., Bonn, 1902. O. Müller, Cucurbitaceae, Cohn's Beiträge, vol. iv. 1887. G. Bitter, Bryonia, Abh. Nat. Ver. Bremen, 1904. (61) M. v. Uexküll-Gyllenband, Phylogenie d. Blütenformen und d. Geschlechtsvert. b. d. Kompositen, Bibl. bot. lii. 1901. A. Tschirch, Kompositen-Antheren, Flora, 1904, li. (62) E. Stahl, Kompasspflanzen, 1883. (63) C. v. Nägeli, Hieracien, Bot. Mitt. iii. 1866. Nägeli, Piloselloiden, *ibid.* 1867. Nägeli, Piloselliformia, *ibid.* 1867. Nägeli, Abstammungslehre, 1884. A. Peter, Hieracium, Engler's Jahrb. v. C. Raunkiaer and C. H. Ostenfeld, Bot. Tidsskr. xxv. 1903. Ostenfeld, Ber. d. D. Bot. Ges. 1904, 376 and 537. O. Rosenberg, Ber. d. D. Bot. Ges. xxiv. 1906, 157. (64) W. Heering, Baccharis (Diss. Kiel) 1899. (65) A. F. W. Schimper, Plant-Geography. (65a) O. H. Juel, Antennaria, Kg. Sv. Vet. Ak. Handl. xxx. 1900. (66) K. Goebel, Pflanzenbiolog. Schilderungen, ii. 1891. (67) The literature cited under 9 and 9a.

SYSTEMATIC INDEX

OF THE

OFFICIAL AND POISONOUS PLANTS

⊙ Official in Great Britain
+ Poisonous
✡ Official and poisonous
* before the page indicates a figure.

Thallophyta

✡ Claviceps purpurea, *395, 397
+ Boletus satanas, 410, *411
+ Amanita muscaria, *412
+ Amanita bulbosa, 412, *413
+ Russula emetica, 413
+ Lactarius torminosus, 413
+ Scleroderma vulgare, *414

Pteridophyta

⊙ Aspidium filix mas, 445, *447, *448, 450
+ Equisetum, *456, 458

Gymnospermae

+ Taxus baccata, *490, *491, 498
⊙ Juniperus communis, *492, 494, 498
+ Juniperus sabina, *493, 494, 498
⊙ Juniperus oxycedrus, 498
⊙ Picea excelsa, *495, 496, 498
⊙ Abies balsamea, 498
⊙ Pinus sylvestris, *497, 498
⊙ Pinus palustris, 498
⊙ Pinus taeda, 498
⊙ Pinus pumilio, 498

Glumiflorae

+ Lolium temulentum, *529, 530
+ Lolium remotum, 530
⊙ Triticum sativum, 530
⊙ Oryza sativa, *529, 530
⊙ Saccharum officinarum, 530

Spadiciflorae

+ Arum maculatum, *535, 536
+ Calla palustris, 536

Liliiflorae

✡ Colchicum autumnale, *537, *538, 543
✡ Schoenocaulon (Sabadilla) officinalis, 543
⊙ Aloe, species of, *540, 543
⊙ Urginea scilla, 543
⊙ Smilax ornata, etc., 543
+ Paris quadrifolia, *542, 543
+ Veratrum album, 541, 543
+ Convallaria majalis, *33, 543
⊙ Crocus sativus, 543, *544

Scitamineae

⊙ Zingiber officinale, 546, *547
⊙ Elettaria cardamomum, 546, 547

Piperinae

⊙ Piper nigrum, *553
⊙ Piper cubeba, *553, 554

Saliciflorae

- ⊙ Salix and Populus, species of, *555, *556

Querciflorae

- ⊙ Quercus infectoria, 653

Urticinae

- ⊙ Ficus carica, *565, 566
- ⊙ Cannabis sativa, 566
- ⊙ Humulus lupulus, *565, 566

Centrospermae

- ⊙ Rheum, species of, 567, *568
- + Agrostemma Githago, *570, 571
- + Saponaria officinalis, *571

Polycarpicae

- + Ranunculus sceleratus, *574, *575
- + Ranunculus arvensis and other species, *574
- + Caltha palustris, 574, *577
- + Anemone pulsatilla, 574, *576
- + Anemone nemorosa, *573, 574
- + Clematis, species of, 574
- + Adonis autumnalis, *573
- + Helleborus, species of, 574, *577
- ✡ Aconitum Napellus, 577, *578
- + Aconitum lycoctonum, and other species, 577, *579
- ⊙ Hydrastis canadensis, 579, *580
- ✡ Delphinium staphisagria, 578
- ⊙ Cimicifuga racemosa, 579
- ⊙ Illicium anisatum, 579
- + Illicium religiosum, 579
- ⊙ Myristica fragrans, 580, *581
- ⊙ Podophyllum peltatum, 580, *581
- ⊙ Jatrorrhiza palmata, 580, *582
- ⊙ Cinnamomum Camphora, 583, 585
- ⊙ Cinnamomum zeylanicum, 583
- ⊙ Sassafras officinale, *583

Rhoeadinae

- ✡ Papaver somniferum, 587
- ⊙ Papaver Rhoeas, *586, 587
- ⊙ Sinapis alba, 591
- ⊙ Brassica nigra, *589, 591
- ⊙ Cochlearia armoracia, 591

Saxifraginae

- ⊙ Liquidambar orientalis, 593
- ⊙ Hamamelis virginiana, 593

Rosiflorae

- ⊙ Rosa gallica, 598
- ⊙ Rosa damascena, 599
- ⊙ Prunus amygdalus, 598, 599
- ⊙ Prunus serotina, 599
- ✡ Prunus laurocerasus, 598, 599
- ⊙ Hagenia abyssinica, *596, 597, 599
- ✡ Quillaja Saponaria, *595, 599

Leguminosae

- ⊙ Acacia senegal, *599, 602
- ⊙ Cassia angustifolia, *601, 602, 605
- ⊙ Cassia acutifolia, 605
- ⊙ Cassia fistula, 605
- ⊙ Copaïfera Langsdorfii, *603, 605
- ⊙ Tamarindus indica, *602, *603, 605
- ⊙ Haematoxylon campechianum, 605
- ⊙ Krameria triandra, *604, 605
- + Cytisus laburnum, *606, 607, 609
- + Cytisus, other species of, 609
- + Coronilla varia, *609
- + Wistaria sinensis, 609
- ⊙ Astragalus gummifer, *607, 609
- ⊙ Glycyrrhiza glabra, *608, 609
- ⊙ Spartium scoparium, 609
- ✡ Physostigma venosum, 609
- ⊙ Andira araroba, 609
- ⊙ Pterocarpus santalinus, 609
- ⊙ Pterocarpus marsupium, 609
- ⊙ Myroxylon toluifera, 609
- ⊙ Myroxylon Pereirae, *604, 605, 606 609

Gruinales

- ⊙ Linum usitatissimum, *611
- ⊙ Erythroxylon Coca, *611
- ⊙ Guiacum officinale, 611
- ✡ Citrus vulgaris, *612
- ⊙ Citrus aurantium, var. Bigaradia, 614
- ⊙ Citrus medica, var. limonum, 614
- ⊙ Barosma betulina, 614
- ⊙ Cusparia febrifuga, 614
- ⊙ Pilocarpus jaborandi, 614
- ⊙ Picrasma excelsa, 614
- ⊙ Quassia amara, *613, 614
- ⊙ Balsamodendron myrrha, 614
- ⊙ Polygala senega, *614, 615

Tricoccae

- + Mercurialis annua, *615
- + Euphorbia, species of, *616, *617
- ⊙ Croton Eleuteria, 618
- ⊙ Croton tiglium, 618
- ⊙ Ricinus communis, 617, *618, *619

Sapindinae

+ Buxus sempervirens, 619
+ Rhus toxicodendron, 619
+ Euonymus europaeus, *620

Frangulinae

⊙ Rhamnus purshianus, 623
⊙ Vitis vinifera, 623

Columniferae

⊙ Theobroma cacao, 624, *625, 626
⊙ Gossypium, species of, *627

Cistiflorae

✲ Garcinia Hanburyi, 628

Thymeläeinae

✲ Daphne Mezereum, *631
✲ Daphne Laureola, 631
✲ Daphne Gnidium, 631

Myrtiflorae

⊙ Eugenia caryophyllata, 633, *634
⊙ Pimenta officinalis, 634
⊙ Melaleuca leucadendron, 634
⊙ Eucalyptus globulus, 632, 634
⊙ Punica granatum, *635

Umbelliflorae

+ Hedera helix, 636, *637
✲ Conium maculatum, *642
⊙ Ferula foetida, 642
⊙ Ferula galbaniflua, 642
⊙ Dorema ammoniacum, 643
⊙ Pimpinella anisum, *637, 643
⊙ Coriandrum sativum, *637, 643
⊙ Foeniculum capillaceum, 643
⊙ Carum carvi, *638, 643
⊙ Anethum (Peucedanum) graveolens, 643
⊙ Ferula sumbul, 643
+ Cicuta virosa, *640
+ Sium latifolium, *639, 641
+ Oenanthe fistulosa, *638, 641
+ Aethusa cynapium, *644, 641
+ Berula angustifolia, 641

Hysterophyta

⊙ Santalum album, 644
+ Viscum album, *644

Ericinae

⊙ Arctostaphylos Uva ursi, *646
+ Rhododendron, 646
+ Azalea, 646
+ Ledum, 646

Diospyrinae

+ Styrax Benzoin, 646

Primulinae

+ Cyclamen europaeum, *648
+ Anagallis arvensis, *648
+ Primula obconica, 648
+ Primula sinensis, 649

Contortae

⊙ Olea europaea, 649, *650, *651
✲ Strychnos nux-vomica, 649, *652
⊙ Gelsemium nitidum, 649
⊙ Gentiana lutea, and other species, 651, *652
⊙ Swertia chirata, 651
+ Menyanthes trifoliata, 651
⊙ Strophanthus kombe, 651
⊙ Strophanthus hispidus, 651, *653
+ Nerium Oleander, 651, *654
+ Vincetoxicum officinale, 654, *655
⊙ Hemidesmus indicus, 656

Tubiflorae

⊙ Exogonium purga, *656, 657
⊙ Convolvulus Scammonia, 657
⊙ Lavandula vera, *658, 660
⊙ Galeopsis ochroleuca, *658, 660
⊙ Rosmarinus officinalis, 660
⊙ Mentha piperita, 660
⊙ Mentha viridis, 660
⊙ Mentha arvensis, 660
⊙ Thymus vulgaris, 660
⊙ Monarda punctata, 660

Personatae

+ Nicotiana tabacum, 663, *665, *666
+ Lycopersicum esculentum, 661
+ Solanum dulcamara, 661, *663
+ Solanum tuberosum, 661
+ Solanum nigrum, 661
✲ Hyoscyamus niger, 663, *667
✲ Datura stramonium, 661, 663, *664
✲ Atropa Belladonna, 661, *662, 663
⊙ Capsicum minimum, 663
✲ Digitalis purpurea, 666, *668, *669

Rubiinae

⊙ Cinchona succirubra, *671, *672, 673
⊙ Uragoga Ipecacuanha, 673, *674
⊙ Ourouparia gambir, 673
⊙ Sambucus nigra, 675, *676
⊙ Valeriana officinalis, 675, *676

Campanulinae

⊙ Lobelia inflata, *677
⊙ Citrullus Colocynthis, 678, *679
⊙ Ecballium elaterium, *678
+ Bryonia dioica, *678

Aggregatae

⊙ Anacyclus Pyrethrum, 688
⊙ Artemisia maritima, var. Stechmanniana, 688
⊙ Anthemis nobilis, 688
⊙ Taraxacum officinale, *683, *684, 688
⊙ Arnica montana, *681, *687, 688

INDEX

(*Asterisks denote Illustrations*)

Abies, *494, 496
Abietoideae, 494
Absciss layers, 150
Absorption, 193
Absorptive powers of soil, 199
Acacia, *599, *600 ; gum, 71, 98
  phyllode, 45, 163, *210 ; seedling, *162 ; *sphaerocephala* (ant-plant), *235
Acaciae Gummi, 602
Acanthaceae, 668
Acanthorhiza, root-thorns, 49
Acanthus, 668
Accessory shoots, 20
Acer, 620, *621 ; leaf, *32 ; *striatum*, epidermis, 146
Aceraceae, 620
Acetabularia, *360
Acetic acid, 80
Achene; *520
Achillea, *505, 688
Achimenes, 666
Achlya, *381
Achnanthes, 350
Acid substances excreted from roots, 200
Aconiti radix, 578
Aconitine, 226
Aconitum, *505, *573, 577, *578, *579 ; exotropism, *282
Acorus, *502, *534, 536 ; ethereal oil, 79 ; root, 121, *114
Acrocomia, fruit, *322
Actaea, 577
Actinomorphic flowers, 507 ; symmetry, 15
Adiantum edgeworthii, budding, 31
Adonis, *573
Adventitious embryos, 302 ; formations, 248 ; roots, 47 ; shoots, 20
Æcidium, 404, *405
Aerating roots, 49
Aerial roots, 46
Aerobionts, 242
Aerotropism, 286
Aeschynanthus, 666
Æsculin, 80, 226
Æsculus, *508, 620 ; bud-scales, 37 ; colleters, 109
Æstivation, 38
Aethusa, *641
African Oil palm, see *Elaeis*
Agaricineae, 412
Agathis, 496
Agave, 213, 543
Aggeratum, 682
Aggregatae, 679
Agrimonia, 597
Agrostemma, *570, 571
Agrostis, 530
Aira, 530
Aitionomic movements, 272
Ajuga, 659
Albugo, 382, *383
Albumen crystals, 77
Albuminous substances, formation of, 221
Alburnum, 133
Alchemilla, *506, *594, 597 ; apogamy, 93, 517 ; exudation of water from, 209
Alcoholase, 223
Aldrovanda, 591
Alectorolophus, 666
Aleurone, 76
Algae, 329 ; assimilation in, 217 ; form, 13 ; fossil, 465 ; selective power, 194
Alisma, *518, 523
Alismaceae, 523
Alkaloids, 80, 226
Alkanet, *Anchusa*
Allium, 541 ; buds, 20 ; mucilage, 79 ; roots, *119, 121
Allochlorophyll, 62
Allotypic division, 86
Alnus, *557 ; root tubercles, 232
Aloe, 213, *540, 543 ; epidermis, *103 ; thickening, 144
Aloes barbadensis, 543 ; socotrina, 543
Alopecurus, 530

Alpine plants, 213
Alpine Rose, *Rhododendron*
Alpinia, 547
Alsineae, 571
Alsophila, *446, *448
Alternation of Generations, 164, 422 ; in Phanerogams, 476 ; in Rhodophyceae, 376 ; in Thallophyta, 331 ; scheme of, 477
Althaea, *504, *626
Aluminium in plants, 187, 192
Amanita, *412, 413
Amarantaceae, anomalous thickening, *143
Amarantus, vascular bundles, 124
Amaryllidaceae, 543
Amber, 98
Amber fir, *Picea succinifera*
Amicia, movements, *294
Amides, 80, 222
Amitotic division, 87
Ammoniacum, 643
Amoebae, symbiosis with algae, 235
Amoeboid movements, *265
Ampelopsis, *27, *622, 623 ; tendril, *27, 44, *289
Amplexicaul leaves, 33
Amygdala amara, 599 ; dulcis, 599
Amygdalin, 80, 226
Amyloerythrin, 76
Amylopectin, 75
Amylum, 530
Anabaena, 339, 452
Anacardiaceae, 619
Anacyclus, 688
Anaerobic respiration, 241
Anaerobionts, 242
Anagallis, *519, *648
Analogous parts, 9
Ananassa, 546
Anaphase, 84
Anaptychia, *420
Anatomy, 52
Anatropous ovules, *472
Anchusa, 658
Andira, 609
Andreaea, *434, 436
Andreaeaceae, 436
Androecium, 502
Andromeda, 646
Andropogon, 529
Aneimia, *448
Anemone, *573, 574, 575 ; adventitious shoots, 20
Anemophilous plants, 306
Anethi fructus, 643
Anethum, 641, 643
Aneura, apical cell, 155
Angiopteris, 445
Angiospermae, 478, 501 ; fertilisation, 91, *92 ; fossil, 688
Angraecum, 48
Anhalonium, 631
Animals, defence against, 116
Anise, *Illicium anisatum*, *Pimpinella*
Anisi stellati fructus, 579
Anisotropy, 273
Annual rings, 131, *132
Annularia, 466
Annulus, of fern, 448 ; of musci, 436
Anona, 579
Anonaceae, 579
Ant-plants, 235
Antennaria, 686 ; apogamy, 93
Anthemideae, 688
Anthemidis flores, 688
Anthemis, 688
Anther, *476, 502
Antheridia, *371, *372, 375, 421, 424, *449
Anthoceros, *429
Anthocerotaceae, 428 ; stomata, 154
Anthocyanin, 80
Anthoxanthum, 530
Anthriscus, 641
Anthurium, 535
Anthyllis, 607
Anticlinal walls, 156
Antimony in plants, 187
Antipodal cells, 514
Antirrhineae, 664
Antirrhinum, *519, 665
Apical cells, *155
Apium, 641
Apocarpous gynaeceum, 503
Apocynaceae, 651 ; latex cells, 72
Apogamy, 93, 303, 517
Apophysis, 436
Apothecium, *392, 393, *418, 419
Apposition, 254
Aqua aurantii floris, 614 ; rosae, 599
Aquifoliaceae, 619
Aquilegia, *573, 577
Araceae, 534 ; climbing roots, 48 ; epiphytic, 213 ; heat produced by respiration, 244 ; pollination, 308 ; velamen, 109
Arachis, 609 ; *hypogaea*, 257, 285
Aralia, cauline bundles, 126
Araliaceae, 636
Araroba, 609
Araucaria, 496 ; wood, 132
Arbor Vitae, *Thuja occidentalis*
Arbuteae, 646
Archaeocalamites, 466
Archangelica, 641
Archegoniatae, 421
Archegonium, 421, *422, 424, *450
Archeplasm, 59
Archetypes, 3
Arctic plants, 213
Arctostaphylos, *646
Arcyria, *341
Areca, 532

Arenaria, 571
Arenga, 534
Argemone, 586
Arillus, *474
Aristolochia, *643, 644 ; flowers, *312 ; stem, *118, *128 ; vascular bundles, *129
Aristolochiaceae, 643
Armeria, *505, 649
Armillaria, *400, *409
Armoraciae radix, 591
Arnica, *680, *681, *687, 688
Arnicae rhizoma, 688
Aroideae, internal hairs, 116
Arrhenatherum, 530
Arsenic in plants, 187
Artemisia, *685, 688
Artichoke, *Cynara* ; Jerusalem, *Helianthus tuberosus*
Artocarpus, 566
Arum, *535, 536
Asafetida, 642
Asarum, 644
Ascent of water, 203
Asclepiadaceae, 653 ; latex cells, 72
Asclepias, *655
Ascobolus, 393
Ascolichenes, 418
Ascomycetes, 387, 388 ; free cell formation in, 91
Ascus, *90, *387 ; development of, *393
Asexual generation of Bryophyta, 424
Asexual reproduction, 298
Ash, 187, 193
Ash, *Fraxinus*
Asparageae, 538
Asparagin, 80, 201, 222
Asparagus, 543 ; root epidermis, 109
Aspergillus, *371 ; *fumigatus*, 233
Asperula, 673, *675
Aspidistra, respiration in, 240
Aspidium, *439, *447, 448, 450
Asplenium, 251 ; leaf runners, 44 ; *Nidus*, 213 ; vegetative reproduction, *302
Assimilation, 214-220 ; specific energy of, 220 ; Engelmann's method of demonstrating, 266
Aster, 686
Astereae, 685
Astragaleae, 607
Astragalus, *607, 608, 609 ; gum, 71
Astrantia, 640
Asymmetrical members, 16 ; flowers, 508
Atavism, 165
Atmospheric pressure, 204
Atriplex, *570
Atropa, 661, *662, 663
Atropine, 226, 663
Atropous ovules, *472
Attraction sphere, 53
Aurantii cortex recens, 614 ; siccatus, 614
Auricula, central cylinder, 120
Auricularieae, 408
Autonomic movements, 272
Auxanometer, *255, 256
Auxiliary cells, 376
Auxospores, *348
Avena, 528, 530 ; starch grains, *74
Avicennia, 659 ; respiratory root, *246
Axial wood, 143
Axile placentation, 504
Axillary shoots, 20 ; buds, traces of, 124
Axis, 22
Azolla, 452
Azotobacter, 189, 232, 337
Azygospores, 384

Baccharis, 686
Bacillus, *333, *334 ; *radicicola*, 232, 337 ; *subtilis*, *333
Bacteria, 331 ; form, 12 ; fossil, 466 ; effect on substratum of, 232 ; phosphorescent, 246
Bacteriastrum, *350
Bacterioids, 232
Bacterium, 335
Baiera, 501
Balanophora, 645 ; apogamy, 303
Balanophoraceae, 645
Balata, 646
Balsaminaceae, 611
Balsamodendron, 614
Balsamum peruvianum, 609 ; tolutanum, 609
Bamboo, *Bambusa*
Bambusa, 530 ; rate of growth of, 255
Banana, *Musa*
Banyan, *Ficus bengalensis*, *Ficus indica*
Barberry, *Berberis vulgaris*
Barium in plants, 187
Bark, 148
Barley, *Hordeum*
Barosma, 614
Bartsia, 231, 666
Basidiobolus, 386
Basidiobolaceae, 386
Basidiolichenes, 420
Basidiomycetes, 387, 400
Basidium, 388, *400
Bast, 138
Batrachospermum, *375, 376
Beaked Parsley, *Anthriscus*
Beech, *Fagus*
Beet, *Beta*
Beggiatoae, sulphur in, 79
Begonia, 47, 630 ; adventitious roots, 47 ; cauline bundles, 126
Begoniaceae, 630 ; epidermis, 109
Belladonnae folia, 663 ; radix, 663
Benzoinum, 646
Berberidaceae, 580
Berberis, 580 ; thorns, 45

Berry, *520
Bertholletia, albumen crystals, 77 ; fat, 78
Berula, 641
Beta, 568, *569 ; etiolation, 259
Betula, *557, 558 ; bark, 149
Betulaceae, 557
Betulin, 149
Bicollateral bundles, 113
Bidens, 687
Bignoniaceae, 666 ; anomalous thickening, *143, *144
Bilateral flowers, 508 ; symmetry, 16
Biophytum, 610
Birch, *Betula*
Bird Cherry, *Prunus avium*
Bird's Nest, *Monotropa*
Bird's-nest Orchid, *Neottia*
Bisymmetrical flowers, 508
Bitter principles, 80, 226
Blackberry, *Rubus*
Blackthorn, *Prunus spinosa*
Blasia, *14, *429
Bleeding of plants, 201
Blepharoplasts, 61
Boehmeria, 566
Bogbean, *Menyanthes*
Boletus, 410, *411 ; tissues, *97
Borage, *Borago*
Boraginaceae, 657
Borago, *657, 658
Bordered pits, 67
Boron in plants, 187
Bostryx, *512
Boswellia, 614
Botrychium, 443, *444
Botrydium, *352
Boudiera, 389
Bovista, 414
Bracken, *Pteris aquilina*
Bract, 37, 509 ; scale, 495
Bracteal leaves, 31, 37
Bracteole, 509
Branch systems, *17
Branched pits, 66
Brand spores, *401
Brassica, *588, *589, 590 ; adventitious shoots, 20
Brazil nut, *Bertholletia*
Bread-fruit, *Artocarpus*
Bristles, 105
Briza, 530
Bromeliaceae, 544 ; climbing roots, 48 ; epiphytes, 213
Bromus, 530
Bromine in plants, 187
Broom, *Spartium*
Brown Algae, Phaeophyceae, 365
Brucine, 226
Bruguiera, 632
Bryinae, 436 ; acrocarpae, 438 ; pleurocarpae, 438 ; stomata, 154
Bryonia, *678
Bryony, *Bryonia*, *Tamus*
Bryophyllum, 592 ; buds, 21
Bryophyta, 421 ; form, 14 ; fossil, 466 ; structure, 153
Bryopsis, 251, 361
Buchu folia, 614
Buckwheat, *Fagopyrum*
Bud, 19, *22, *252 ; metamorphosis of, 23 ; resting, 22 ; scales, 22, *36, 37, 101
Budding, 251, *252 ; multiplication by, 301
Bugloss, *Echium*
Bulb, *24
Bulbils, *23, *28, 301
Bulbochaete, 358, *359
Bundles, bicollateral, 113 ; cauline, 126 ; collateral, 113 ; common, 126 ; concentric, 113 ; course of, 123-126 ; foliar, 126 ; open, 114 ; terminations of, 114
Bupleurum, 640
Burdock, *Lappa*
Burnet Saxifrage, *Pimpinella*
Burseraceae, 614
Butomus, 524
Butter-bur, *Petasites*
Buttress roots, *185
Buxaceae, 619
Buxus, 619

Cabbage, *Brassica*
Cabomba, *573
Cactaceae, 73, 630
Cactus, 27
Caesalpinia, wood, 133
Caesalpiniaceae, 602
Caffeine, 226, 628
Calamarieae, 466
Calamogrostis, 530
Calamostachys, 466
Calcicolous plants, 191
Calcium in plants, 187, 188, 190
Calcium carbonate, 71, 133 ; excretion of, 104
Calcium oxalate, 71, 73, 78
Calendula, 688
Calenduleae, 688
Calla, 536
Callithamnion, *375
Callitrichaceae, 618
Callose, 69
Calluna, 645
Callus, 151 ; -wood, 151
Calobryaceae, 431
Calobryum, 431
Caltha, 574, *577
Calumbae radix, 588
Calyptra, 15, 46, 436
Calyptrogen, 159

Calystegia, 657
Calyx, 502
Cambium, 128, *129, 131, 142
Cambogia, 628
Campanula, *677 ; epidermal cell, *67 ; silica, 71
Campanulaceae, 675
Campanulinae, 675
Camphora, 583
Camptosorus, leaf-runners, 44
Campylospermae, 641
Campylotropous ovules, *472
Canadian Waterweed, *Elodea*
Cananga, 579
Canarium, 614
Canna, *507, *548 ; starch grains, 74
Cannabinaceae, 566
Cannabis, 566
Cannabis indica, 566
Cannaceae, 547
Cantharellus, 412
Caoutchouc, 79, 227, 617, 651
Capillarity, 204
Capillitium, 340
Capitulum, *510
Capparidaceae, 591
Capparis, *590, 591
Caprifoliaceae, 674
Capsella, *474, *518, *588, 591 ; Heegeri, 306
Capsici Fructus, 663
Capsicum, 661, 663
Capsule, 436, 519
Caragana, 609
Carbon, 187 ; absorption, 214-220 ; in plants, 188, 189 ; monoxide, 220
Carbonic acid gas, source of, 215
Cardamine, *588 ; adventitious shoots, 20
Cardamom, 547
Cardinal points, 176 ; of temperature, 258
Carduus, *680, 681, *682
Carex, 525, *526
Carica, 630
Caricaceae, 630
Carnivorous plants, 236
Carotin, 63
Carpel, 37, 472
Carpinus, 558, *559 ; seedling, *161, *198
Carpodinus, 651
Carpogonium, 376, *377, 388, *419
Carrot, *Daucus Carota*
Carroway, *Carum*
Carui fructus, 643
Carum, *638, 640, 641, 643
Caruncula, 615
Carya, 555
Caryophyllaceae, 570
Caryophyllum, 634
Caryopsis, 520, 527
Cascara Sagrada, 623
Cascarilla, 618
Cassia, *601, 602, 605
Cassiae pulpa, 605
Cassytha, 583
Castanea, *561, 562
Castilloa, 565
Casuarinaceae, 555
Catalpa, 666
Catechu, 673
Catkin, 509, *511
Caulerpa, 360, *361 ; organs, 249 ; structure, 152
Cauline bundles, 126
Cecidia, 165
Cecidomyia, 166
Cecropia, 235
Cedrus, 498
Celandine, *Chelidonium*
Celastraceae, 620
Celery, *Apium*
Cell, *52 ; budding, 91 ; division, *82, 87 ; duration of life of, 263 ; filament surface and masses, 154 ; forms, 71 ; fusions, 93 ; internal pressure of, 179 ; multinucleate, 60, 89 ; nucleus, 59 ; ontogeny of the, 80 ; -plate, 88 ; -sap, 53, 79 ; size of, 73 ; uninuclear, 89 ; -wall, 63, 88
Cell-wall, growth of, 254 ; insertion of, 157 ; thickening of, *64
Cellular plants, 154
Cellulose, 69
Celtis, 563
Centaurea, 682 ; movements, *296
Centaury, *Erythraea*
Central cylinder, 113, 117, 160
Centranthus, 675
Centricae, 349
Centriole, 53, 61, 86
Centrosome, 53, 61, 86, 91
Centrospermae, 566
Cephalanthera, 549
Cephalanthus, 672
Cephalotus, 238, 593
Cerastium, *513, 571
Ceratophyllaceae, 573
Ceratophyllum, 49, 197, 573
Ceratium, *343
Ceratozamia, *482, 485, *486
Cercis, *601, 605
Cereus, *630
Cerinthe, 658
Ceriops, 632
Ceropegia, latex, 73
Ceroxylon, wax, 101
Cetraria, *417, *418, 421
Chaerophyllum, 641
Chaetocladium, 385
Chalaza, 472
Chalazogamy, *515, *516
Chara, *363, *364 ; parthenogenesis, 93, 365 ; spermatozoid, *92

Characeae, 59; cell-wall, 71; direct nuclear division, 87
Chasmogamous flowers, 309
Cheiranthus, *588, 590
Cheirostrobus, 467
Chelidonium, *475, 586; *laciniatum*, 300; laticiferous vessels, 94
Chemotactic movements, 266
Chemotropic curvatures, 286
Chemotropism, 286
Chenopodiaceae, 567; anomalous thickening of, *143
Chenopodium, 570
Cherry, *Prunus Cerasus*
Chervil, *Chaerophyllum*
Chinese Primrose, *Primula sinensis*
Chirata, 651
Chiropterophilous plants, 308
Chlamydomonas, *353
Chlamydospores, 388
Chloramoeba, *351
Chlorella, *356
Chlorine, in plants, 187, 191
Chlorococcum, *355
Chlorophyceae, 353
Chlorophyll, 61, 62, 217; grains, *93, *268; preparation of solution of, 61
Chloroplasts, *61, 93
Chlorotic, 191
Choanephora, 385
Cholesterin, 78
Chondrioderma, *55, 341
Chondromyces, *337
Chondrus, *373, 378
Chorda, *368
Choripetalae, 552
Chromatin, 57, 59, 81
Chromium in plants, 187
Chromoplasts, 61, *63
Chromosomes, 81, *82, *83, *85, 92, 164; individuality of, 83
Chroococcus, 339, 420
Chroolepideae, 357
Chrysanthemum, 688
Chrysarobinum, 609
Chrysobalaneae, 598
Chytridiaceae, 380
Cibotium, 450
Cichorieae, 682
Cichorium, *682
Cicuta, *640, 641
Cilia, 265, 332
Cimicifuga, *573, 579
Cimicifugae rhizoma, 578
Cinchona, *671, *672, 673
Cinchonae rubrae cortex, 673
Cinchoneae, 671
Cincinnus, *512
Cinnamomi Cortex, 683
Cinnamomum, 582, *585, 688; ethereal oil, 79
Cinnamon tree, *Cinnamomum*
Circulation of protoplasm, 58, 267
Circumnutation, 272
Circaea, 632
Cirsium, 681
Cissus, 623
Cistaceae, 629
Cistiflorae, 627
Cistus, 629
Citrullus, 678, *679
Citrus, *612, 613, 614; ethereal oil, 98
Cladodes, 25
Cladonia, *418, *419
Cladophora, 359, *360; cell, *60; cell division, *89; *glomerata*, *12
Cladostephus, apical cells, 155; *verticillatus*, *12
Cladothrix, *333, 334
Classes of Phanerogams, 478
Classification, 327
Clavaria, *410
Clavarieae, 410
Claviceps, *395, 397; tissue, *98
Cleft leaves, 33
Cleistocarpae, see Phascaceae
Cleistogamous flowers, 309
Cleistogamy, 518
Clematis, 574; cell, *64; vascular system, 124, *126
Clerodendron, 659
Climbing plants, 30
Climbing roots, 48, 249
Closterium, *346
Clostridium, 189, *234
Clover, *Trifolium*
Cloves, 634
Cnicus, 682, *683
Cobaea, 657
Cobalt, reaction, 208; in plants, 187
Cocae folia, 611
Cocaine, 226, 611
Cocconeïs, *349
Cochineal, 631
Cochlearia, *589, 591
Coco-nut, *Cocos*
Cocoa tree, *Theobroma*
Cocos, *531, *532
Codeine, 226
Coelospermae, 642
Cœnogametes, 379
Coffea, 672, *673
Coffeae, 672
Coffee, *Coffea*
Cohesion, movements dependent on, 270
Cola, 625
Colchicine, 226
Colchicum, *537, *538, 543; tuber, 25
Coleochaete, 359
Collateral bundles, 113
Collema, *419
Collenchyma, 68, 116, 118, 185

Colleters, *108
Colletia, 623 ; *cruciata*, spines, 28
Colocasia, exudation of water from, 210
Colocynthidis pulpa, 678
Colouring matters, 226
Colours of flowers, 80
Coltsfoot, *Tussilago*
Columella, 433
Column, 549
Columniferae, 623
Colutea, 609
Combretaceae, 632
Comfrey, *Symphytum*
Commelinaceae, 536
Commiphora, 614
Common bundles, 126
Companion cells, *95, 112, 137
Compass plants, 278
Complementary cells, 149
Compositae, 680 ; inulin, 80 ; laticiferous, vessels, 94 ; pappus, 271
Compound leaves, 33
Concentric bundles, *115, 113
Conferva, 351, *352
Conidia, 388
Coniferae, 489 ; medullary rays, 140 ; red wood, 186 ; resin ducts, 98 ; *132 ; white wood, 186
Coniferin, 70, 80, 226
Conii, folia, 642 ; fructus, 642
Coniine, 226
Conium, *637, *642
Conjugatae, 344
Conjugation, 91, 346
Connate leaves, 33
Connecting fibres, 87
Connective, 503
Consortium, 415
Constituents of plant substance, 187
Constitution water, 196
Contact stimuli, curvatures induced by, 287
Contortae, 649
Contractile vacuole, 56
Convallaria, 33, 543
Convolvulaceae, 656
Convolvulus, *656, 657 ; adventitious shoots, 20
Copaiba, 605
Copaifera, *603, 605
Copper in plants, 187
Cora, *420
Corallorhiza, 49, 231, 549 ; rhizome of, *24
Corchorus, 623
Cordaites, 500
Cordyline, 543 ; thickening, *145
Corethron, 351
Coriandri fructus, 643
Coriandrum, *637, 642, 643
Cork, *52, *147 ; cambium, 146
Cork Oak, *Quercus suber*
Cormophytes, 14
Cormus, 14
Corn Cockle, *Agrostemma*
Cornaceae, 635
Cornus, *636
Corolla, 502
Coronilla, *609
Cortex, 117, 146, 160
Corydalis, *475, *508, *586, 587
Corylus, *511, 558, *560 ; adventitious shoots, 20
Corypha, 262
Cosmarium, *345
Cotton, *Gossypium*
Cotton grass, *Eriophorum*
Cotyledons, 162, 473
Crambe, *588
Crassula, 592
Crassulaceae, 592 ; epithema, 123
Crataegus, *552, 595 ; leaf, 207 ; thorn, 28
Crenothrix, 334
Crepis, 682
Cribraria, 342
Crinum, root epidermis, 109
Crocus, 543, 544 ; tuber, 25
Croton, 616, 618
Crown Imperial, *Fritillaria*
Cruciferae, 587 ; mucilage, 71 ; idioblasts, 73
Cryptogams, 328
Cryptospora, *394
Cubebae fructus, 554
Cucumber, *Cucumis sativus*
Cucumis, 678
Cucurbita, 678 ; etiolation, 259 ; pollen grain, *503 ; rate of growth of, 255 ; seedling, *285 ; sieve-tubes, *95 ; tactile pits, *65 ; vascular bundles, 124
Cucurbitaceae, 677 ; bicollateral bundles, 113
Cupressineae, 492
Cupule, 559, *560
Cupuliferae, 559
Curvature, 269 ; autonomic, 272 ; dependent on growth, 272 ; dependent on imbibition, 270 ; due to variations in light and temperature, 290 ; heliotropic, 276 ; paratonic, 272
Cuscuta, 657 ; *europaea*, 228, *229 ; haustoria, 249 ; reduction of leaves, 27 ; root, 46
Cusparia, 614
Cuspariae cortex, 614
Cusso, 599
Cuticle, 100 ; regeneration of, 71
Cutinisation, 70
Cutleriaceae, 369
Cuttings, 251

Cyanophyceae, 337
Cyatheaceae, 449
Cyathium, *614
Cycadaceae, 484 ; spermatozoids, 91
Cycadinae, 484
Cycadofilices, 466, 500
Cycas, 484, *485, *486
Cyclamen, *648 ; regeneration, 152
Cycle, 42
Cyclosporeae, 370
Cydonia, 595 ; mucilage, 71
Cylindrocystis, 345
Cymose inflorescences, 510
Cynara, 682
Cynareae, 681
Cyperaceae, 524 ; sheath, 36 ; silicae, 191
Cyperus, 525
Cypress, _Cupressus_
Cypripedium, 549
Cystocarp, 376
Cystoliths, *68
Cystopus, _Albugo_
Cytisus, *604, *606, 607, 609, _adami_, *317
Cytoplasm, 53, 57

Dactylis, 530
Dahlia, 687 ; inulin, 80 ; root tubers, *47
Dandelion, _Taraxacum_
Daphne, *631
Darlingtonia, 238, 591
Date palm, _Phoenix_
Datura, 661, 663, *664
Daucus, 641 ; chromoplasts, *63
Decurrent leaves, 33
Delphinium, *504, 577, 578
Dentaria, bulbils, *23
Dermatogen, 157
Desert plants, 211 ; excretion of water by, 211
Desiccation, 195
Desmidiaceae, 345 ; movements, 266
Desmodium, movements, 292
Deutzia, 593
Development of the shoot, 18
Dextrorse stem climbers, *284
Diageotropism, 281
Diakinesis, 84
Diandrae, 549
Dianthus, 571
Diapensia, *504
Diatomeae, 347 ; form, 12 ; silicon, 191 ; movements, 266
Diastase, 223
Diatropism, 274
Dicentra, 587
Dichasium, *512, *513
Dichogamy, 310
Dichotomosiphon, 361
Dicotylae, 551
Dicotyledons, 113 ; central cylinder, 118 ; medullary rays, 139 ; phloem of, 139 ; secondary thickening of, *142 ; secondary wood, 134 ; vascular bundle, 114, 124 ; venation, 35
Dichotomous branch system, 17
Dichotomy, 18 ; false, 18
Dictamnus, 612
Dictyonema, 420
Dictyota, *13, *370 ; apical cell, 155
Dictyotaceae, 370
Diervilla, 675
Differentiation, 171
Digenetic reproduction, 298
Digestive glands, 211
Digitalin, 226
Digitalis, 665, *668, *669 ; folia, 666
Dill, _Anethum_
Dinoflagellata, see Peridineae
Diœcious plants, 309
Dionaea, 237, 591 ; leaf, *238 ; movements, 295
Dioscorea, *544
Dioscoreaceae, 544 ; thickening, 144 ; tubers, 49, *50
Diospyrinae, 646
Diospyros, 646
Diplocaulescent, 28
Diplococcus, 336
Diploid, 165
Diplostemonous androecium, 507
Dipsacaceae, 680
Dipsacus, 680
Dipterocarpaceae, 628
Direct nuclear division, 87
Dischidia Rafflesiana, 213, 656 ;
Discomycetes, 391
Dissemination of seeds, 318
Divergence of leaves, 41
Diversiflorae, 682
Divided leaves, 33
Dodder, _Cuscuta_
Dorema, 643
Dormant buds, 23
Doronicum, 688
Dorsiventral, flowers, 508 ; shoots, 42 ; symmetry, 16
Dorstenia, 564
Double fertilisation, 305
Draba verna, petites espèces, 300
Dracaena, *541, 543, 688 ; raphides, *77 ; thickening, 144, *145, *146
Drepanium, *512
Drimys, 552 ; wood, 136
Drip tips, 35
Drosera, 236, 591 ; digestive glands, 107, 108, 109 ; leaf, *238
Droseraceae, 591
Drosophyllum, 591
Drupe, 520
Dryas, 597

Dryobalanops, 638
Dryophyllum, 689
Duckweed, *Lemna*
Dudresnaya, 376, *377
Duramen, 133
Duration of life, 261, 262

Ebenaceae, 646
Ecballium, *678
Echinocactus, 630
Echinodorus, *523
Echinops, 681
Echium, *657, 658
Ectocarpus, *369
Edelweiss, *Leontopodium*
Egg, 91 ; -apparatus, 514
Eichhornia, 196
Elaeagnaceae, 631
Elaeagnus, 631 ; root tubercles, 232
Elaeis, 533
Elaphomyces, 397
Elasticity of plants, 178
Elaterium, 678
Elder, *Sambucus*
Electrotropism, 286
Elettaria, *474, 547
Elodea, 524
Elongation, phase of, 253
Embryo, 473, 516, *518 ; of fern, 439
Embryology, 154
Embryonic phase of growth, 248
Embryo sac, 472, *514 ; nuclear division in, 90
Emergences, 50, 105, 107
Empusa, *385, 386
Enantioblastae, 536
Endocarp, 519
Endocarpon, 418
Endodermis, 117, *120
Endogenous, 20
Endophyllum, *400
Endosperm, 473, 516 ; nucleus, 516
Endothecium, 503
Energy, respiration as a source of, 242
Enteromorpha, *357
Entire leaves, 33
Entomophilous plants, 307
Entomophthorineae, 385
Enzymes, 223
Ephedra, *498, *499 ; free cell formation, 91
Ephemerum, *434
Epiblem, 100
Epidermis, 100, *100, 160
Epigeal germination, 323
Epigynous flowers, *505, 506
Epilobium, 632
Epinasty, 272
Epipactis, 549 ; cell division, *88
Epiphyllum, 631
Epiphytes, aerial roots, 48
Epipogon, 549
Epithema, 123
Equisetaceae, apical cell, 156 ; central cylinder, 118 ; epidermis, 100 ; silicon, 71, 191 ; spores, 271
Equisetinae, 455 ; fossil, 466
Equisetum, *455, *456, *457, 458, 466 ; vegetative cone, *156, *157
Ergot, *Claviceps*
Erica, 645
Ericaceae, 645
Ericeae, 645
Ericinae, 645
Erigeron, 686
Eriobotrya, 595
Eriophorum, *525
Erodium, 610 ; fruit, *271
Ervum, 609
Eryngium, 640
Erysiphe, ascospore formation, *90
Erysipheae, 389, 390
Erythraea, 651, *652
Erythroxylaceae, 611
Erythroxylon, *611
Escholtzia, 586
Espeletia, 687
Ethereal oils, 79, 98, 226
Etiolation, *259
Eucalypti gummi, 634
Eucalyptus, 632, 634, 688; heterophylly, 35
Eucheuma, 378
Eudorina, 355
Eugenia, 633, *634
Euglena, *339
Eumycetes, 386
Euonymus, *620 ; vegetative cone, *30
Eupatorieae, 682
Eupatorium, 682
Euphorbia, 27, *615, *616, *617 ; succulent stems, *212
Euphorbiaceae, 615 ; caoutchouc, 78 ; latex cells, 72
Euphrasia, 231, 666 ; haustoria, 49
Euryale, 573
Eusporangiatae, 443
Everlasting flowers, *Helichrysum*
Evolution, theory of, 1, 175
Exine, 475
Exoasci, 398
Exoascus, 398
Exobasidium, 409
Exocarp, 519
Exodermis, 120
Exogenous, 20
Exogonium, *656, 657
Exothecium, 503
Exotropism, 281, *282
External influences, irritability to, 273 ; upon growth, 257
Extrorse anthers, 503
Exudation of water, *209

Faba, 609
Fagopyrum, *505, *520, 567 ; water culture, *190
Fagus, 559, *561 ; leaf, *122 ; medullary rays, 141 ; splint wood, 133 ; winter buds, *22
Fall of the leaves, 150
Fascicular cambium, 129
Fats, 78
Fennel, *Foeniculum*
Fermentation, 233, 243
Ferments, 78, 79, 223
Ferns, *Filicinae*, adventitious shoots, 20 ; apical cell, 156 ; apogamy, 303 ; apospory, 304 ; climbing roots, 48 ; concentric bundles, *115 ; epiphytic, 213 ; heterophylly, 35 ; leaf-runners, 43 ; petiole, 123 ; phosphorescence, 247 ; root apex, *158 ; scale hairs, 107 ; stomata, 104 ; vessels, 96
Fertilisation, 164, 304, 305, *515, *516, *517
Ferula, 641, 642, 643
Festuca, 212, *527, 530
Fibre, *72, 81, 136 ; -tracheides, 72, 135
Fibro-vascular bundles, 111
Fibrous cells, 136, 139
Ficus, 564, *565 ; *indica*, 49 ; pollination, 308 ; cystoliths, *68, 71, 109 ; epidermis, 109 ; stipules, 37
Fig, *Ficus*
Filago, 686
Filament, 502
Filices, 445
Filicinae, 443 ; fossil, 466
Filix mas, 450
Fir, *Picea*
Flagella, 265
Flagellata, 339
Flax, *Linum*
Floral, diagram, *40, *508 ; formula, 508; leaf structure, 121 ; leaves, 31, 37 ; shoots, 28 ; symmetry, 507
Florideae, *see* Rhodophyceae
Flowers, 28, *502 ; colour of, 80 ; development in darkness, 259 ; of Angiospermae, 501 ; of Gymnospermae, 480 ; opening and closing of, 291
Fluctuating variations, 165, 300
Fluorine in plants, 187
Foeniculi fructus, 643
Foeniculum, *505, *637, 641, 643
Foliage leaves, 31 ; structure of, 121, *122 ; metamorphosis of, 43
Foliage shoots, 28
Foliar bundles, 126
Follicle, 519
Fontinalis, 438
Food of plants, constituents of, 188
Fool's parsley, *Aethusa*
Foot, 436, 440
Forget-me-not, *Myosotis*
Formic acid, 80
Fossil Angiosperms, 688 ; Cryptogams, 465 ; Gymnosperms, 500
Foxglove, *Digitalis*
Fragraria, 597
Frangulinae, 621
Fraxinus, 649, *650
Free, cell formation, 90 ; central placentation, 504 ; leaves, 38 ; nuclear division, 89
Freycinetia, 530
Fritillaria, 543 ; leaves, 40
Fructus Anisi, 643
Fruit, *519 ; dehiscence of, 270 ; enlargement of, 127 ; epidermis, 109
Frullania, *430 ; water-sacs, 213
Fucaceae, 367, 371
Fuchsia, 632
Fucosan, 368
Fucus, *367, *371, *372 ; centriole, 61, *86, *87 ; nucleus, *53, *86, *87
Fuligo, 341
Fumaria, *520, 587
Fumariaceae, 587
Funaria, *61, *91, *423, 438
Fundamental tissue system, 100, 115
Fungi, cell fusions, 96 ; effect on substratum of, 232 ; glycogen, 78 ; nutrition of, 234 ; phosphorescent, 246 ; structure, 152 ; tissues, 97
Fungus gardens, 235
Funiculus, 472
Funkia, *516 ; adventitious embryos, *303
Furze, *Ulex*

Galanthus, 543
Galbanum, 642
Galegeae, 607
Galeopsis, *658, 659
Galium, *520, 673 ; stipules, 36
Galls, 165, 563
Gametes, 91, 331
Gametophyte, 164, 439
Garcinia, 628
Gaseous exchange, mechanism of, 221
Gasteromycetes, 413
Geaster, *414
Gelsemii radix, 649
Gelsemium, 649
Gemmae, 23, *426
Generation, alternation of, 164 ; diploid, 165 ; haploid, 165
Generative cells, 476
Genetic spiral, 42
Genista, 213, 607
Genisteae, 607
Gentiana, 649, 651, *652
Gentianaceae, 649
Gentianae radix, 651

Geotropic, curvature, *280, *281 ; variation movements, 293
Geotropism, 278
Geraniaceae, 610
Geranium, *507, *610
Germination, 161, 162, 318, 320, 474
Gesneriaceae, 666
Geum, 597
Gigartina, *374, 378
Ginger, *Zingiber*, 547
Ginkgo, *481, *488, *489 ; spermatozoids, 91
Ginkgoaceae, 488
Ginkgoinae, 488
Gladiolus, 543
Glands, 108
Glandular hair, *107, 108
Glaucium, *585
Gleba, 413
Glechoma, 659
Gleditschia, 232, 605 ; buds, 20 ; thorns, *27, 28
Globoid, *76
Gloeocapsa, *11, *338
Gloxinia, 666
Glucose, 79, 195, 218, 221
Glucosides, 80, 225
Glume, 526
Glumiflorae, 524
Glutamin, 80
Glycogen, 78
Glycyrrhiza, *608, 609
Glycyrrhizae radix, 609
Gnaphalium, 686
Gnetaceae, 498 ; vessels, 96
Gnetinae, 498
Gnetum, 498, *499, *500 ; anomalous thickening, *143
Gonidia of Lichens, 416
Goniodoma, *343
Gossypium, 626, *627 ; hairs, 105, *106
Gossypium, 627
Gracilaria, 378
Graft-hybrids, 252, 318
Grafting, 251, *252
Gramineae, *526 ; epidermis, 100 ; root apex, *159; silica, 71, 191; sheath, 35
Granati cortex, 635
Grand periods of growth, 254, 256
Granular plasma, 58
Grape vine, *Vitis*
Graphis, 418
Grass haulm, curvature of, 284, *285
Gratiola, 665, *667
Gravity, irritability to, 279; reaction to, 174
Ground nut, *Arachis hypogaea*
Growing point, 154
Growth, 247-263 ; by apposition, 64 ; by intussusception, 64 ; correlation of, 249 ; curvatures, 272 ; influence of light on, 258 ; influence of moisture on, 260 ; influence of temperature on, 257 ; intercalary, 22 ; in thickness, 128, *131, 142 ; limited, 30 ; of cell wall, 64 ; mechanical influence on, 260 ; phases of, 248 ; unlimited, 30
Gruinales, 610
Guarana, 620
Guard cells, 103, 206
Guiaci, lignum, 611 ; resina, 611
Guiacum, 611
Gum, 70, 98
Gummosis, 70
Gunnera, central cylinder, 120
Gutta percha, 79, 227, 646, 652
Guttiferae, 628
Gymnadenia, 549
Gymnocladus, buds, 20
Gymnodinium, *343
Gymnogramme, 101
Gymnospermae, 113, 478, 480 ; fertilisation, 91 ; secondary wood, 134, 142 ; central cylinder, 118 ; fossil, 500 ; medullary rays, 139 ; phloem, 138 ; root apex, 159 ; vascular bundles, 114, 124
Gymnosporangium, *405
Gynaeceum, 502
Gynandrae, 548
Gynostemium, 549
Gyromitra, 394

Haastia, 686
Habit of plants, 29
Hadromal, 70, 112
Haematococcus, *354
Haematoxyli lignum, 605
Haematoxylon, 133, 605
Haemoglobin, 62
Hagenia, *596, 597
Hairs, see Trichomes
Halimeda, 361
Halophytes, *192
Halorrhagidaceae, 632
Hamamelidaceae, 593
Hamamelidis cortex, 593 ; folia, 593
Hancornia, 651
Haplocaulescent, 28
Haploid, 165
Haplomitrium, *430, 431
Haplostemonous androecium, 507
Harveyella, 378
Haustoria, 49, *229
Hazel, *Corylus*
Heart-wood, 133
Hedera, 636, *637
Hedychium, 547
Hedysareae, 609
Heliantheae, 686
Helianthemum, *628, *629
Helianthus, *517, *682, 687 ; tuber, 25
Helichrysum, 686

Heliotactic movement, 277
Heliotropism, 274, 275
Heliotropium, 658
Helleborus, *36, 574, *577 ; epidermis, *102 ; stoma, *206
Helobiae, 522
Helvellaceae, 394
Hemerocallis, *476
Hemidesmi radix, 656
Hemidesmus, 656
Hemlock, *Conium*
Hepaticae, 424, 425 ; apical cell, 155 ; conducting strands, 110 ; elaters, 271 ; form, 14
Herbs, 29
Hercogamy, 311
Herniaria, 571
Hesperidin, 80
Heterobasidion, 412
Heterocontae, 351
Heterodynamic hybrids, 313
Heterœcious Uredineae, 406
Heterogenesis, 300
Heteromerous Lichens, 416
Heterophylly, 35
Heterosporous Pteridophyta, 441
Heterospory, 471
Heterostyly, 310
Heterotype division, 86
Hevea, 617
Hibisceae, 626
Hibiscus, 626
Hieracium, *682 ; apogamy, 93, 518 ; apospory, 518
Hilum, 474
Hippocastanaceae, 620
Hippophäe, 631
Hippuris, 632 ; vegetative cone, *157
Histology, 52
Holcus, 530
Homodynamic hybrids, 313
Homoiomerous Lichens, 416
Homology, 9
Homosporous Pteridophyta, 441
Homotype division, 86
Honeysuckle, *Lonicera*
Hoodia, 656
Hop, *Humulus*
Hordeum, 528 ; root apex, *159
Hornbeam, *Carpinus*
Horse-chestnut, *Aesculus*
Horse-tail, *Equisetum*
Hoya, 656
Humboldtia, 235, *236, 605
Humulus, *565, 566 ; glandular hair, 107, 108
Humus, 199 ; plants, 231
Hura, fruit, 320
Hyacinthus, 541
Hyaloplasm, 58
Hybridisation, 313, *315
Hydathodes, 108, 123, 210
Hydneae, 410
Hydnophytum, 672
Hydnum, *410
Hydra, symbiosis with algae, 234
Hydrangea, 593
Hydrastine, 579
Hydrastis, 579, *580
Hydrastis rhizoma, 579
Hydrocharis, 524
Hydrocharitaceae, 524
Hydrocotyle, 640
Hydrocyanic acid, 226
Hydrodictyon, 356
Hydrogen, in plants, 187, 188, 189
Hydrolapathum, *13 ; structure, 152
Hydrophilous plants, 307
Hydrophyllaceae, 657
Hydropterideae, 450, 466
Hydrotropism, 286
Hygroscopic movements, 271
Hylocomium, 438
Hymenolichenes, 420
Hymenomycetes, 408
Hymenophyllaceae, 449
Hyoscyami folia, 663
Hyoscyamus, *474, 663, *667
Hypecoum, 587
Hypericum, *628
Hyphae, 255, 383 ; rate of growth of, 255
Hyphaene, 530
Hypholoma, *400
Hypnum, *435, 438
Hypocotyl, 162
Hypoderma, 118, 121
Hypogeal germination, 323
Hypogynous, *505, 506
Hyponasty, 272
Hypophysis, 516
Hysterophyta, 643

Iberis, 591
Ice, formation of, in tissues, 176
Idioblasts, 73, 116
Ilex, *619
Illicium, 579 ; ethereal oil, 79
Imbibition, movements dependent on, 270 ; water, 194
Imbricated leaves, 38
Impatiens, 611 ; bundles, 109 ; *116 ; collenchyma, *67
India-rubber tree, *Ficus*
Indian cress, *Tropaeolum*
Indian hemp, *Cannabis*
Indican, 226
Indigofera, 609
Indirect nuclear division, 81
Indusium, 448
Inflorescence, 509
Insectivorae, 591
Insectivorous plants, 43, 227, 236

Integuments, 472
Intercalary growth, 257
Intercellular spaces, 97, 98, 244
Interfascicular cambium, 129
Internal, development of organs, 248, 260 ; hairs, 116 ; morphology, 52 ; structure, the phylogeny of, 152
Internodes, 22
Intine, 475
Intramolecular respiration, 241
Intussusception, 254
Introrse anthers, 503
Inula, 686
Inuleae, 686
Inulin, 80
Iodine, in plants, 187, 373 ; reaction, *218
Ipecacuanha, 673
Ipomoea, 657
Iriartea, root hairs, 49
Iridaceae, 543 ; diagram, *40, *41
Iris, 543, *545 ; root, *120
Iron, bacteria, 243, 335 ; in plants, 187, 188, 190
Irritability, 4, 174, 273
Isatin, 226
Isatis, 591
Isoetaceae, 464
Isoetes, *464, *465 ; desiccation, 195
Isogamous fertilisation, 331
Isosmotic coefficients, 180
Ivy, *Hedera*

Jaborandi folia, 614
Jalapa, 657
Jambosa, 633
Jasione, 677
Jasminum, 649
Jatrorrhiza, 580, *582
Juglandaceae, 554
Juglandiflorae, 554
Juglans, *516, *554, 555
Juncaceae, 538
Juncaginaceae, 524
Juncus, *536, 538
Jungermanniaceae, 429
Juniperus, *492, *493 ; vascular system, 123, *124
Juvenile form, 163

Kalmia, *313
Kandelia seedling, *321
Karyokinesis, 81
Kickxia, 651
Kino, 609
Kinoplasm, 59, 88
Kleinia articulata, 213
Klinostat, 256
Knautia, 680
Knots, 144
Krameria, *604, 605
Krameriae radix, 605

Labiatae, 659
Labiatiflorae, 682
Laboulbeniaceae, 388, *398
Laburnum adami, *317
Lachnea, *392
Lactarius, 412
Lactuca, 682 ; *scariola*, 277 ; laticiferous vessels, 94
Lagenostoma, 509
Lamina, 31
Laminaria, *366
Laminariaceae, 366 ; sieve-tubes, 110 ; structure, 153
Lamium, *657, 659
Landolphia, 651
Lantana, 659
Laportea, 566
Lappa, *681, 682
Larch, *Larix*
Larix, *481, 496 ; short shoots, 21
Latent buds, 23
Lateral, geotropism, 281 ; roots, 47
Latex, 73, 98, 227 ; cells, *72
Lathraea, 665 ; albumen crystals, 77 ; exudation of water, 210
Lathyrus, 609 ; stipules, 44 ; tendrils, 44, 45, *163
Laticiferous vessels, 94, *96
Laudatea, 420
Lauraceae, 580
Laurocerasi folia, 599
Laurus, 582, *584 ; ethereal oil, 79
Lavandula, 658, 660
Lead in plants, 187
Leaf, base, 31, 35 ; blade, 31 ; cushion, 33 ; development of, 30, 31 ; foliage, 32 ; forms of, 31 ; mechanical tissues of, *184 ; rigidity of, *185 ; scars, 38, 150 ; sheath, 31, 35 ; stalk, 31 ; symmetry of, *16 ; tendrils, 44 ; tip, 31 ; thorns, 45 ; traces, 123 ; venation, *207
Leaves, arrangement of, 39 ; autumnal changes, 62 ; fall of the, 150 ; of mosses, 432 ; origin of, 160 ; reduction of, 213 ; secondary growth of, 145 ; structure of, 121 ; succulent, 213
Ledum, 646
Legume, 519
Leguminosae, 599 ; aluminium, 192 ; root tubercles, 232
Lemna, 536 ; chlorophyll grains, *268 ; root pocket, 46
Lemnaceae, 536
Lentibulariaceae, 668
Lenticels, *149, 244
Leocarpus, *342
Leontodon, flower head, *291
Leontopodium, 686
Lepidium, *588

Lepidodendreae, 466
Lepidostrobus, 467
Lepiota, 412
Leptome, 112
Leptomin, 79
Leptosporangiatae, 445
Leptothrix, *11, 335
Lessonia, 336
Lettuce, *Lactuca*
Leucadendron, 212
Leucobryum, 432
Leucojum, 543 ; *544
Leuconostoc, *334
Leucoplasts, 61, 63
Levisticum, 641
Lianes, 30 ; vessels, 96, 137, 202
Libriform fibres, 136
Lichenes, 415 ; aluminium, 192 ; composition of thallus, 234
Licmophora, 348
Life, conditions of, 172
Light, effect in photosynthesis, 216 ; influence on growth, 258 ; irritability to, 274
Lignification, 70
Lignified cell walls, 69
Ligule, *34, 526
Liguliflorae, 682
Ligustrum, 649
Liliaceae, 538 ; diagram, 40 ; raphides, 78
Lilieae, 538
Liliiflorae, 536 ; secondary growth of, 127
Lilium, *85, *517, 541 ; bulbils, 23 ; nuclear division, 85
Lily, *Lilium* ; of the Valley, *Convallaria*
Lime, *Tilia*
Lime scales, 211
Limnanthemum, 651
Limonis cortex, 614 ; succus, 614
Linaceae, 610
Linaria, *511, 665 ; *cymbalaria*, 257 ; heliotropism, 278
Linin, 59
Linum, *505, 610, *611
Linum, 611
Liquidambar, 593
Liriodendron, 579
Listera, 549
Lithium in plants, 187
Litorella, 668
Liverworts, *Hepaticae*
Loasaceae, stinging hairs, 106
Lobed leaves, 33
Lobelia, *504, *677
Lobelia, 677
Lobeliaceae, 677
Loculicidal dehiscence, 519
Locust, *Robina pseudacacia*
Lodicules, 526
Lodoicea seychellarum, 178
Loganiaceae, 649
Lolium, *529, 530
Lonicera, 674 ; buds, 20 ; leaves, 33
Lonicereae, 674
Lophospermum, *290
Loranthaceae, 644
Loranthus, 644
Loteae, 607
Lotus, *604, 607
Lovage, *Levisticum*
Linaria, *588
Lupinus, 607
Lupulin, 108
Lupulinum, 566
Lupulus, 566
Luzula, 538
Lychnis, 571 ; *viscaria*, 101
Lycoperdon, *414
Lycopersicum, 661
Lycopodiaceae, 46, 459 ; dichotomy, 19
Lycopodinae, 458, 466 ; growing point, 157 ; root apex, 158
Lycopodium, *19, *440, *459, *460 ; aluminium, 192 ; central cylinder, 113
Lycoris, root epidermis, 109
Lyginodendron, 500
Lyginopterideae, 500
Lygodium, growth of leaf, 30
Lysimachia, 648
Lythraceae, 632
Lythrum, 632

Maclura, wood, 133
Macrocystis, *366
Macrosporangia, 441, *453, 472
Macrospore, 441, *453, 463, 472
Macrosporophyll, 472
Magnesium in plants, 187, 188
Magnolia, 579
Magnoliaceae, 579
Maianthemum, 543
Maize, *Zea*
Malacophilous plants, 308
Malic acid, 80
Mallotus, 618
Maltose, 221
Malva, *625, *626 ; heliotropism, 277 ; mucilage, 71 ; pollen-grain, *503
Malvaceae, 626
Malveae, 626
Mamillaria, 630
Manganese in plants, 187
Mangifera, 619
Mangosteen, *Garcinia*
Mangrove, roots, 49 ; seedlings, *321
Manihot, 617
Mannite, 373
Mantle leaves, 35
Maples, *Acer*
Maquis, 660
Maranta, 547
Marantaceae, 547

Marattiaceae, 445 ; pseudo-periderm, 148
Marchantia, *421, *422, *426, *427 ; air-pore, 152 ; gemmae, 249
Marchantiaceae, 426
Marrubium, 660
Marsilia, *451, 466 ; parthenogenesis, 93, 303
Marsiliaceae, 451
Matricaria, *681, *685, 688
Matthiola, 590
Maximum, intensity of stimulus, 175 ; temperature, 258
Mechanical, influence on growth, 260 ; rigidity of plants, 116 ; tissues, 182, *183
Meconopsis, 286
Median plane, 508
Medicago, 607
Medlar, *Mespilus*
Medulla, 117, 118
Medullary rays, 118, *130, *138, 139, 140 ; sheath, 131
Medulloseae, 500
Melaleuca, 634
Melampyrum, 231, 666
Melanthieae, 538
Melastomaceae, 632
Melica, 530
Melilotus, 607
Melissa, *660
Melon, *Cucumis Melo*
Melosira, 350
Members of independent origin, 15, 49
Mendel's laws, 314
Menispermaceae, 580
Mentha, 660
Menthol, 660
Menyanthes, 651
Mercurialis, *615, 616 ; epidermis, *102
Mercury in plants, 187
Meristem, 99
Merogony, 304
Merulius, 412
Mesembryanthemum, 213
Mesocarp, 519
Mesocarpus, orientation of chloroplasts, 268
Mesophyll, 121 ; sheath, 122
Mesotaeniaceae, 344
Mesotaenium, 345
Mespilus, 595
Mestome, 111
Metabolism, 186, 225
Metamorphosis, 10 ; of the bud, 23 ; of foliage leaves, 43; of primary members, 15 ; of roots, 48 ; theory of, 15
Metaphase, 84
Metaplasm, 57
Metroxylon, 533
Metzgeria, 429 ; apex, 155
Mezerei cortex, 631
Micellae, 254
Micrasterias, *345
Micrococcus, *11
Micropyle, 472
Microsomes, 58
Microsporangia, *441, *453, 475
Microspores, 441, *453, 462, 475
Microsporophylls, 475
Middle lamella, 69, 98
Midsummer growth, 131
Mignonette, *Reseda*
Milfoil, *Achillea*
Millet, *Andropogon*
Millon's reagent, 57
Mimosa,* 599, 600 ; leaf, 34 ; movements, 293, *294, 295
Mimosaeae, 599
Mimusops, 646
Mineral substances, 195 ; absorption of, 195
Minimum intensity of stimulus, 175 ; temperature, 258
Mistletoe, *Viscum album*
Mitotic nuclear division, 81
Mnium, conducting strands, 110 ; stem, *153
Moisture, influence on growth, 260
Molinia stem, *183
Monandrae, 549
Monarda, 660
Monkshood, *Aconitum*
Monoblepharideae, 379
Monoblepharis, *379
Monochasium, 512
Monocotylae, 521
Monocotyledons, central cylinder, 118 ; secondary growth, 127, 144 ; vascular bundles, 114, 125 ; venation, 35
Monoecious plants, 310
Monogenetic reproduction, 298
Monopodial branch system, 17
Monopodium, 17
Monotropa, 646
Monotropeae saprophytic, 231
Monstera, 534 ; leaf, 35
Monstrosities, 165 ; causes of, 166
Moraceae, 563 ; caoutchouc, 79 ; latex cells, 72
Morchella, *393, 394 ; ascus, *387
Morphine, 226
Morphology, 6, 9, 10
Morus, *521, 563
Moss capsule, 424
Mosses, *Musci*
Mousetail, *Myosurus*
Movement, phenomena of, 263-296
Mucilage, 70, 79 ; tubes, 94
Mucilaginous cell walls, 70 ; sheath, 321
Mucor, 383, *384, *385
Mucorineae, 383
Mucuna, anomalous thickening, *143

Mulberry tree, *Morus*
Mullein, *Verbascum*
Multicellular hairs, 107
Multilateral symmetry, 15
Multinucleate cells, 60
Musa, 546 ; leaf, 35, 184
Musaceae, 546
Muscari, 541 ; buds, 20
Muscarine, 226
Musci, 426, 431 ; apical cell, 156 ; constructing strand, 110 ; stem, *153
Mushroom, *Psalliota campestris*
Mustard, *Sinapis*
Mutations, 3, 300
Mutisieae, 682
Mycelium, 386
Mycorhiza, 231
Myrmecophytes, 235
Myosotis, 658 ; dorsiventral shoots, 43
Myosurus, 574
Myrica, 555 ; wax, 101
Myricaceae, 555
Myriophyllum, 632
Myristica, *475, 579, 580, *581 ; fat, 78
Myristicaceae, 579
Myrmecodia, *237, 672
Myrobalans, 632
Myronic acid, 226
Myroxylon, *604, *605, 606, 609
Myrrha, 614
Myrsiphyllum, *284
Myrtaceae, 632
Myrtiflorae, 631
Myrtle, *Myrtus*
Myrtus, 632, *634
Myxamoeba, 341
Myxobacteriaceae, 337
Myxococcus, 337
Myxomycete, 54, 96, 340

Naiadaceae, 524
Naias, 524
Narcissus, 543
Nastic curvatures, 270
Nasturtium, adventitious shoots, 20
Natural selection, theory of, 2
Navicula, *348
Neckera, 438
Nectaries, 102, 109, 211, 507
Nectria, 395, 397
Negative, geotropism, 279 ; heliotropism, 275
Nelumbium, 196, 573
Neottia, 62, 231, 549
Nepenthaceae, 591
Nepenthes, *43, 591 ; leaf, *238
Nepeta, 659
Nephromium, 420
Nerium, 651, *654 ; stomata, 154
Nervature, *see* Venation
Nest leaves, 35
Netted veined leaves, 34
Nettles, *Urtica*
Nickel in plants, 187
Nicotiana, *505, 662, *665, *666
Nicotine, 226
Nightshade, *Solanum nigrum* ; Enchanter's, *Circaea* ; Deadly, *Atropa*
Nitella, 363 ; turgidity, *180 ; rotation of protoplasm, 59, 267
Nitragin, 232
Nitrate bacteria, *Nitrobacter*
Nitrite bacteria, *Nitrosomonas*
Nitrobacter, *337
Nitrogen, 187 ; fixation of, 187, 232 ; in plants, 188, 189
Nitrosomonas, *337, 243
Nitzschia, 351
Nodes, 22
Normal shoots, 20
Nostoc, *338 ; symbiotic, 429
Nucellus, 472
Nuclear, cavities, 83 ; division, 81-87, *82 ; division, allotypic, 86 ; division, direct, 87 ; division, indirect, 81 ; division, heterotype, *85, 86 ; division homotype, 86 ; division, mitotic, 81 ; membrane, 60 ; network, 81 ; plate, *82 ; sap, 60 ; spindle, 81, *83, *85
Nucleoli, 59, 82
Nucleus, *53 ; albumen, crystals in, 77
Nuphar, 572
Nut, *520
Nutations, 272
Nutmeg, *Myristica*
Nutrition, 186 ; special processes of, 227
Nux Vomica, 649
Nyctaginaceae, anomalous thickening, *143
Nyctitropic movements, 293
Nymphaea, *475, *572, *573
Nymphaeaceae, 572 ; internal hairs, 116

Oak, *Quercus*
Oat, *Avena sativa*
Obturator, 615
Ochrea, 37, *567
Ocimum, 660
Odontites, 666 ; haustoria, 49
Odontospermum, 686
Oedogonium, 358, *359
Oenanthe, *638, 641
Oenothera, *632 ; *lamarckiana*, 300
Oidium Tuckeri, 390
Oil-ducts, 98
Oils, 78, 225
Olea, 649, *650, *651 ; latent buds, 23
Oleaceae, 649 ; albumen crystals, 77
Oleander, *Nerium oleander*
Oleum, cadinum, 498 ; cajaputi, 634 ; crotonis, 618 ; eucalypti, 634 ; juniperi, 498 ; lavandulae, 660 ; menthae

piperitae, 660 ; menthae viridis, 660 ; olivae, 649 ; pini, 498 ; ricini, 618 ; rosae, 599 ; rosmarini, 660 ; santali, 644 ; terebinthinae, 498 ; theobromatis, 626
Olibanum, 614
Olive, *Olea*
Olpidium, *381
Onagraceae, 632
Onoclea, 446 ; spermatozoid, *92
Ononis, 607
Ontogeny, 2, 9 ; of the internal structure, 154 ; of the cell, 80 ; repeating phylogeny, 162
Oogamous fertilisation, 331
Oogonia, 331, *371
Oomycetes, 379
Oosphere, 331
Oospore, 331
Ophioglossaceae, 443
Ophioglossum, 443, *444, *445 ; adventitious shoots, 47 ; cork, 148
Ophrys, 549
Optical apparatus, 102
Optimum, intensity of stimulus, 176 ; temperature, 258
Opuntia, *26, 630, 631 ; cladodes, 26
Orchidaceae, 73, 548 ; aerial roots, 48 ; climbing roots, 48 ; epiphytes, 213 ; mucilage, 71, 79 ; raphides, 78 ; root tubers, 48 ; siliceous bodies, 78 ; velamen, 109
Orchis, *48, *548, *549, *550
Organic, acids, 80, 225 ; compounds, synthesis of, 5
Organography, 10
Orientation, 267
Origanum, 660
Ornithocercus, *343
Ornithogalum, *539, 541 ; cell wall, 71 ; endosperm, *66
Ornithophilous plants, 308
Ornithopus, 609
Orobanchaceae, 666
Orobanche, 229, 666, *670
Orthospermae, 639
Orthostichies, 41
Orthotropic, 273
Oryza, 76, *529 ; starch, 75
Oscillaria, *338, 339
Osmosis, 179, 195, 204
Osmotic pressure, 180
Osmunda, *448
Osmundaceae, 449
Ostrich fern, *Struthiopteris*
Ourouparia, 672, 673
Ovule, *472
Ovuliferous scale, 495
Ovum, 514
Oxalic acid, 80
Oxalidaceae, 610
Oxalis, 610 ; movements, 292 ; organic acid, 80
Oxydases, 223
Oxygen, 187 ; in plants, 188, 189 ; liberated in photosynthesis, *219

Padina, 370
Paeonia, *502, 577 ; flower, *38
Palaquium, 646, *647
Palea, 526
Palisade cells, 121, 122 ; parenchyma, *122
Palmae, 530 ; secondary growth of, 127 ; type of vascular system, 125, 126 ; siliceous bodies, 78 ; stability, 178 ; wax, 101
Palmate leaves, 33
Pandanaceae, 530 ; secondary growth of, 127
Pandanus, 530, *533 ; adventitious roots, 49 ; leaves, 40
Pandorina, 355
Panicle, *510, *511
Panicum, 529
Pansy, *Viola tricolor*
Papaver, *475, *586, 587 ; laticiferous vessels, 94 ; vascular bundles, 124
Papaveraceae, 585
Papaveris capsulae, 587
Papaw, *Carica papaya*
Papilionaceae, 605 ; tendrils, 44
Papillae, 105
Parallel-veined leaves, 34, *522
Paramecium, symbiosis with algæ, 234
Para nuts, *Bertholletia excelsa*
Parasites, 227 ; reduction of shoot in, 27
Parastichies, 41
Paratonic movements, 272
Parenchyma, 99, 112
Parietal placentation, 504
Paris, *542, 543
Parnassia, 593
Paronychieae, 571
Parsley, *Petroselinum*
Parsnip, *Pastinaca*
Parthenogenesis, 93, 303, 365
Partial fruits, 519
Partite leaves, 33
Passiflora, *504, 630
Passifloraceae, 630
Pastinaca, 641
Paullinia, 620 ; anomalous thickening, *143
Payena, 646
Pea, *Pisum*
Pectin compounds, 99
Pedate leaves, 34
Pediastrum, *356
Pedicularis, 231, 666
Peireskia, 630
Pelargonium, *610

Pellia, 429
Peltate leaves, 43
Peltigera, 420
Penicillium, *391 ; selective power, 195
Pennatae, 349
Pentacyclicae, 645
Pepper, *Piper nigrum*
Perfoliate leaves, 33
Perianth, 40
Periaxial wood, 144
Periblem, 157
Pericarp, 519
Perichaetium, 433
Periclinal walls, 156
Pericyle, 118
Periderm, 145
Peridineae, 342
Peridinium, *343
Peridium of the Uredineae, 404 ; of Gasteromycetes, 413
Perigynous flowers, *505, 506
Periodicity in development, 261
Periplasm, 441
Perisperm, 473
Perisporiaceae, 389
Perisporieae, 390
Peristome, 436, *437, *438
Perithecium, *390, *394
Periwinkle, *Vinca*
Permanent tissue, 99
Peronospora, 382, *383
Peronosporeae, 381
Persea, *582, 583
Personatae, 661
Peruvian wax palm, *Ceroxylon andicola*
Petal, 37
Petasites, 688
Petiole, 31 ; structure, 122
Petroselinum, 641
Petunia, *661, 663
Peziza, *392 Phaeophyceae 365
Phaeophyll, 62, 368
Phaeosporeae, 368
Phajus, leucoplasts, *75
Phalloideae, 415
Phallus, *414, 415
Phanerogam, growing point, 157
Phanerogamia, 471
Pharbitis, 283, *284
Phascaceae, 436
Phascum, *423
Phaseoleae, 609
Phaseolus, 609 ; growth, 257 ; starch grains, *74
Phelloderm, 147
Phellogen, 146
Philadelphus, 593
Phleum, 530
Phloem, 112, *141 ; parenchyma, 113 ; secondary, 137
Phloeoterma, 117
Phlomis, 660
Phlox, 657
Phoenix, 533
Phormium, leaf, *184
Phosphorescence, 245
Phosphorus in plants, 187, 188, 189
Photometry, 278
Photosynthesis, 216
Phototactic movements, 265
Phragmidium, 405, *406, *407
Phycocyanin, 62
Phycoerythrin, 62, 374
Phycomycetes, 378
Phyllactinia, 390
Phyllocactus, 631
Phylloclades, 25
Phyllode, 45, *162, *163, 210, 212
Phylogeny, 2, 9 ; of the internal structure, 152
Physalis, *520
Physiology, 6, 171
Physodes, 58
Physostigma, 609
Physostigmatis semina, 609
Phytelephas, *94, 225, *473, 533 ; cell wall, 71
Phyteuma, 677
Phytolacca, vascular bundles, 124
Phytolaccaceae, anomalous thickening, *143
Phytopathology, 167
Phytophthora, 381, *382
Phytoteratology, 167
Picea, *482, *483, *495, 396 ; *succinifera*, 98
Picrasma, 614
Pilobolus, 384 ; heliotropism, *276
Pilocarpine, 226
Pilocarpus, 614
Pilostyles, *230
Pilularia, *451
Pimenta, 634
Pimenta, 634
Pimpinella, *637, 640, 643
Pinaceae, 491
Pine, *Pinus*
Pinguicula, 237, 668
Pinks, *Dianthus*
Pinnate leaves, 33
Pinnularia, *11
Pinus, *481, *483, *494, *497 ; bordered pit, *66 ; medullary ray, *135, 140 ; sieve-tubes, *66 ; wood, *130, *132, *136
Piper, *553 ; ethereal oil, 79 ; vascular bundles, 124
Piperaceae, 552 ; epidermis, 109
Piperinae, 552
Pistacia, 619
Pisum, 609 ; tendrils, 44, *45
Pith, 117, 118

Pithecoctenium, seed, *319
Pits; 65 ; branched, 66 ; membrane, 65
Pitted vessels, 95
Pix, burgundica, 498 ; liquida, 498
Placenta, 472, 503
Placentation, *504
Plagiochila, *429, *14
Plagiotropic, 273
Plankton, 351
Planktoniella, *350
Plantaginaceae, 668
Plantago, *511, 668, *670 ; bundles, 110 ; protogyny, *310 ; triplocaulescent, 28
Plantain, *Plantago*
Plants, distinct from animals, 3
Plasmodiophora, 342
Plasmodium, 54, *55, 341
Plasmolysis, 71, 180
Plasmopara, 382
Platananceae, 593
Platanus, 593
Platycerium, 251 ; heterophylly, 35
Plectridium, *334
Pleiochasium, 510
Pleomorphism, 163
Plerome, 157
Pleurocladia, *368
Pleurosigma, 350
Plumbaginaceae, 649
Poa, 530
Podalyrieae, 606
Podophylli rhizoma, 580
Podophyllum, 580, *581
Podospora, *394, 395
Podostemaceae, 591 ; adventitious shoots, 29 ; emergences, 107 ; hapterae, 51 ; roots, 48
Polar, caps, 81 ; nuclei, 514
Polarity, 250
Polemoniaceae, 657
Polemonium, 657
Pollen, chamber, 486 ; grains, 475, *503, *513 ; sacs, 475 ; tube, 476, *481, *513 ; tube, rate of growth of, 255
Pollination, 306
Pollinium, 654
Polyangium, *337
Polyblepharis, *353
Polycarpicae, 571
Polyembryony, 302
Polygala, *614, 615
Polygalaceae, 614
Polygonaceae, 567 ; stipules, 37
Polygonatum, *522, 543 ; rhizome, *23, 24
Polygonum, *514, *515, *567
Polypodium, 446, *449, *450 ; heterophylly, 35
Polyporeae, 410
Polyporus, *411
Polytoma, *353
Polytomy, 18 ; false, 18
Polytrichaceae, conducting strands, 111
Polytrichum, 432, *434, 438
Pomeae, 595
Poplar, *Populus*
Poppy, *Papaver*
Populus, *556 ; adventitious shoots, 20 ; bud, *39
Poricidal, dehiscence, 519
Porogamy, *515
Positive, geotropism, 280 ; heliotropism, 275
Potamogeton, *523
Potamogetonaceae, 524
Potassium in plants, 187, 188
Potato, *Solanum tuberosum*
Potato disease, 381
Potentilla, *506, *594, 597
Potentilleae, 597
Prickles, 107
Primary members, the metamorphosis of, 15
Primary meristem, 99 ; tissue, 100 ; tissues, distribution of, 117
Primitive form of membrane, 10
Primordial, leaf, 31 ; utricle, 54
Primula, glandular hairs, 108 ; heterostyly, *311 ; *sinensis*, *107 ; *sinensis*, glandular hairs, *107
Primulaceae, 647
Primulinae, 647
Privet, *Ligustrum*
Procambium strands, 113, 128
Products of assimilation, transfer of, 222 ; utilisation of, 221
Proembryo, 483, 516
Promeristem, 99
Promycelium, 403
Prophases, 84
Prosenchyma, 99
Proserpinaca, growth, 260
Protandry, 310
Prothallium, *439, 443, *449, 453, *454, *457, 458, 460, *463, *465, 473
Protococcales, 335
Protogyny, *310
Protonema, *423, 431
Protophloem, 114
Protoplasm, 53, 54, 173 ; circulation of, 58 ; inclusions of, 73 ; movements of, 58 ; reactions of, 57 ; rotation of, 58
Protoplast, 53 ; connection of, 93 ; *94 ; differentiation of, 73 ; movements of, 265
Protoxylem, 114
Pruneae, 598
Pruni virginianae cortex, 599
Prunus, *594, *598 ; *avium*, bud scales, *36 ; *cerasus*, 511 ; *cerasus*, gum, 71 98 ; *spinosa*, thorns, 28

Psalliota, *411, 412 ; hypha, *60
Pseudomonas, 335
Pseudoparenchyma, 386
Pseudotsuga, 495
Psidium, 633
Pteridophyta, 113, 438 ; bundles, 113, 126 ; fossil, 466 ; root, 158 ; secondary growth, 127
Pteridospermeae, 500
Pteris, *439, *440, 449 ; concentric bundles, *115 ; petiole, 123 ; root apex, *158 ; vessels, 96
Pterocarpi lignum, 609
Pterocarpus, 609 ; wood, 133
Puccinia, *404, *405 ; pleomorphism, 164
Pulmonaria, 658
Pulvinus, 33, 392
Pumpkin, *Cucurbita pepo*
Punica, 634, *635
Punicaceae, 634
Purple Loosestrife, *Lythrum*
Putrefaction, 233
Pycnidium, *394, 396
Pycnoconidia, 396
Pyrenomycetes, 394
Pyrethri radix, 688
Pyrola, 646
Pyrolaceae, 646
Pyronema, 389, *393 ; fertilisation, *392
Pyrus, *506, *594, *595 ; periderm, *147
Pyxidium, *519, 520

Quassia, *613, 614
Quassiae lignum, 614
Querciflorae, 556
Quercus, *560, *561, *562, *688 ; bark, *150 ; bud scales, 37 ; cork, *150 ; galls, 166 ; latent buds, 23 ; medullary rays, 141 ; midsummer growth, 132 ; *suber*, bark, 148 ; *suber*, cork, 148 ; vessels, 96
Quillaiae cortex, 599
Quillaja, 594, *595
Quinaria tendrils, 289
Quince, *Cydonia*
Quinine, 226, 673

Raceme, 509, *510, *511
Racemose inflorescence, 509, *510
Radial symmetry, 15 ; of flowers, 507
Radial walls, 156
Radium, influence on growth, 259
Radix rhei, 567
Rafflesia, 645 ; reduction of shoot, 27
Rafflesiaceae, 645 ; haustoria, 49 ; parasitism, 229
Ramondia, 666
Ranunculaceae, 573
Ranunculus, *506, *574, *575 ; bundle, *112 ; heterophylly, *34, 35 ; leaf, 35
Raoulia, *210, 686
Raphe, 472
Raphides, *77, 78
Receptacle, 448
Red Algae, Rhodophyceae
Reduced structures, 10
Reduction, division, 84, *85
Regeneration, 151
Rejuvenescence, 65
Reproduction, 296
Reseda, 591 ; multicellular formation, *89
Resedaceae, 591
Reserve, cellulose, *473 ; material, in seed, *473 ; material, storage of, 224
Resin, protective covering of, *209
Resina, 498
Resins, 79, 226
Respiration, 239, *242 ; heat produced by, 244 ; intramolecular, 241 ; movement of gases in, 244
Respiratory cavity, 104 ; coefficient, 241 ; roots, *246
Rest-harrow, *Ononis*
Resting period, 262
Reticulate vessels, 95
Revolving movement, 282
Rhabdonema, 350
Rhachis of leaf, 33
Rhamnaceae, 622
Rhamni Purshiani cortex, 623
Rhamnus, *622, 623
Rheotaxis, 266
Rheotropism, 286
Rheum, 567, *568, *569
Rhinantheae, 665
Rhinanthus, 231
Rhipidium, *512
Rhipsalis, 631
Rhizobium radicicola, 232
Rhizoids, 15, 50 ; of Musci, 432
Rhizomes, 24
Rhizomorpha, 246
Rhizophora, 632, *633
Rhizophoraceae, 632
Rhizophores, 50
Rhizopus, *383 ; streaming protoplasm 268
Rhododendron, *504, 646
Rhodophyceae, 373
Rhodoreae, 646
Rhoeadinae, 585
Rhoeados petala, 587
Rhus, 619
Ribes, *592, 593
Riccia, *14, *425
Ricciaceae, 425
Rice, *Oryza*
Richardia, 536

Ricinus, 617, *618, *619 ; aleurone grains, *76 ; palisade cells, 122
Rigor, cold, heat, etc., 296
Ringed bark, 148
Robinia, 608 ; adventitious shoots, 20 ; leaf, 34 ; movements, 293 ; thorns, *45 ; tyloses, *133
Rocella, 418
Rontgen Rays, influence on growth, 259
Root, 15, 45, *114, *119, *120, 158 ; adventitious, 47 ; aerial, 46 ; apex of, *158, *159 ; branching, 46 ; cap, 15, 46, 158 ; central cylinder, 120 ; contraction of, 323 ; growth of, 256 ; -hairs, 46, 105, 120, *198, 199 ; hypoderma, 121 ; lateral, 161 ; lenticels, 150 ; mechanical tissues of, *184 ; metamorphosis of, 48 ; parasitic, 231 ; phellogen, 149 ; -pocket, 46 ; -pressure, *200, 204 ; primary cortex, 120 ; secondary thickening of, 142 ; -stocks, 24 ; structure of, 120 ; subterranean, 47 ; -system, 198 ; -system length of, 198 ; tubers, *48 ; tubercles, *231, 232 ; vascular strands of, 127
Rosa, *520, *594, 595 ; adventitious shoots, 20 ; prickles, 107 ; stipules, 36
Rosaceae, 593
Rosae Gallicae Petala, 598
Rose, *Rosa*
Rose of Jericho, *Odontospermum*
Roseae, 595
Rosiflorae, 593
Rosmarinus, 660
Rotation of protoplasm, 58, 267
Rozites, 413
Rubia, 673
Rubiaceae, 671
Rubidium in plants, 187
Rubiinae, 668
Rubus, *521, *597 ; adventitious shoots, 20
Rudimentary structures, 10
Rumex, 567 ; adventitious shoots, 20 ; organic acids, 80
Runners, 25
Ruppia, 524
Ruscus, cladode, 25, *26
Russula, hymenium, *408
Rust fungi, Uredineae
Rust of wheat, *Puccinia graminis*
Ruta, *612
Rutaceae, 611
Rye, *Secale*

Saccharomyces, *11, 91, 398, *399 ; cell-budding, 91 ; fermentation, 243 ; zymase, 223
Saccharomycetes, 398
Saccharum, 529, 530 ; wax, *101
Saffron, 544
Sage, *Salvia*
Sagittaria, *523
Salicaceae, 555
Saliciflorae, 555
Salicin, 556
Salicornia, *192 ; organic acids, 80
Salix, *555, 556 ; adventitious roots, 47 ; buds, 23 ; *polaris*, *213
Salpiglossis, 663
Salsola, organic acids, 80
Salvia, *659, 660 ; pollination, *312
Salvinia, 49, *452, *453, *454, 466
Salviniaceae, 452
Sambuceae, 674
Sambuci flores, 675
Sambucus, 674, *676 ; lenticel, *149 ; stem, *183
Samolus, axillary shoot and leaf, *22
Sanguisorba, *594, 597
Sanicula, 640
Santalaceae, 644
Santalin, 133
Santalum, 644
Santoninum, 688
Sap cavities, 53
Sapindaceae, 620
Sapindinae, 618
Saponaria, *571
Saponin, 80
Sapotaceae, 646 ; gutta-percha, 79
Saprolegnia, *380 ; parthenogenesis, 303
Saprolegniaceae, 380
Saprophytes, 227, 231
Sap wood, 133
Sarcina, 336
Sarcocaulon, resinous covering, *209
Sargassum, 367
Sarothamnus, 213, 607
Sarracenia, 238, 591
Sarraceniaceae, 591
Sarsaparilla, 543
Sassafras, *583 ; radix, 583
Satureja, 660
Saxifraga, 593 ; lime scales, 211 ; water stomata, 104
Saxifragaceae, 592
Saxifrage, *Saxifraga*
Saxifraginae, 591
Scabiosa, 680
Scalariform vessels, 95, *96
Scale hairs, 107 ; -leaves, 31, 37
Scaly bark, 148
Scammoniae radix, 657
Scandix, 641
Scenedesmus, *356
Schistostega, *435 ; phosphorescence, *246 ; protonema, *176
Schizaeaceae, 449
Schizocarp, *520
Schizogenic intercellular spaces, 98

Schizomycetes, 332
Schizonema, 348
Schizosaccharomyces, 399
Schoenocaulon, 543
Schulze's macerating mixture, 99
Scilla, 541
Scirpus, *525
Scitamineae, 546
Scleranthus, 571
Sclereides, 67, 73, 116
Sclerenchyma, 72, 116, 182
Scleroderma, 413, *414
Sclerospora, 382
Sclerotia, 56, 386
Sclerotic cells, 184
Scolopendrium, 446, *448, 449
Scorzonera, 682 ; vessels, *96
Scotch Fir, *Pinus Silvestris*
Scrophularia, 665
Scrophulariaceae, 663 ; albumen crystals, 77
Scurvy grass, *Cochlearia*
Scutellaria, *508
Scutellum, *527
Scytonema, 420
Secale, *528
Secondary, growth of Monocotyledons, 127 ; meristem, 99 ; tissue, 100, 127, 152
Sedum, 213, *592
Seed, 473, *474, *475 ; coat, 474 ; desiccation, 196 ; dispersion by animals, 319 ; dispersion by water, 319 ; dissemination of, 318 ; epidermis, 109 ; germination of, 318-320 ; leaves, 162 ; winged, 318
Selaginella, *461, *462, *463 ; desiccation, 195 ; phosphorescence, 247 ; rhizophores, 50, *51 ; vascular bundles, 113
Selaginellaceae, 461
Selection, theory of, 2
Selective power of cells, 194
Selenium in plants, 187
Self-fertilisation, 308
Semi-permeable membrane, 179
Sempervivum, 213, 592
Senecio, 688
Senecioneae, 688
Senegal radix, 615
Senna, 602
Senna, Alexandrina, 605 ; Indica, 605
Sensitive plant, *Mimosa*
Sepal, 37
Septicidal dehiscence, 519
Sequoia, 496
Serjania, anomalous thickening of, 143, *144
Sesleria, 212
Sessile leaves, 32
Seta, 436
Sexual generation of, Angiosperms, 513 ; of Bryophyta, 422 ; of Gymnospermae, 480 ; of Pteridophyta, 439
Sexual organs of Musci, 432
Sexual reproduction, 298, 304
Shade-loving plants, 176
Shoot, 18-29 ; apex, 18, *19 ; branching of, 19 ; development, 18 ; endogenous, 20 ; exogenous, 20 ; origin, 160 ; short, 21 ; subterranean, 23 ; symmetry of, 16
Shorea, 628
Shrubs, 29
Sicyos tendril, *289
Sieve plates, 67, 93 ; tubes, *66, 93, *95, 112, 137, 222
Sigillarieae, 466
Silene, *569, 571
Sileneae, 571
Siler, *673
Silica, 71
Siliceous bodies, 78 ; earth, 192, 351
Silicic acid, 133
Silicon in plants, 187, 191
Siliculosae, 590
Siliqua, 519
Siliquosae, 590
Silphium laciniatum, 277
Silver fir, *Abies*
Silver in plants, 187
Simarubaceae, 614
Simple leaves, 33
Sinapis, 590 ; albae semina, 591 ; nigrae semina, 591
Sinistrorse stem climbers, *283, 284
Siphonales, 360 ; fossil, 465
Siphoneae, 3~~6~~60 ; nuclei, 60 ; tissue, 97
Siphonocladiales, 359
Siphonocladus, 359
Sisymbrium, *588
Sium, *639, 641
Size of cell, 73
Sleep movement, nyctitropic movements
Sleep positions of leaves, 291
Slime fungi, Myxomycetes
Smilax, 543, 688
Smut fungi, Ustilagineae
Snowdrop, *Galanthus*
Sodium in plants, 187, 191
Soil, absorptive power of, 199
Solanaceae, 661
Solanin, 80, 226
Solanum, 661, *663 ; *nigrum*, 661 ; tubers, 25, *26
Solerina, 420
Solidago, 686
Sonchus, 682
Sophoreae, 606
Sorbus, *594, 595
Soredia, 417
Sorghum, starch, 76
Sorus, 448
Spadiciflorae, 530
Spadix, 509

Sparassis, 410
Sparganiaceae, 530
Spartium, 607, 609 ; shoots, 27
Spathodea, exudation of water from, 210
Spergula, 571
Spermaphyta, 478
Spermatium, 376, 388
Spermatozoid, 91, 331, *449, *462, *464, *487 ; chemotaxis of, 266
Spermogonia, 388, 404, *420
Sperms, 478
Sphaeria, 395
Sphaeroplea, 359
Sphaerothallia, 418
Sphaerotheca, *390
Sphagnaceae, 434
Sphagnum, *432, *433
Sphenophyllinae, 467
Sphenophyllum, 467
Spike, 509, *510, *511
Spikelet of Gramineae, *526, *527
Spinach, *Spinacia*
Spinacia, 75, 568 ; starch, 75
Spindle, fibres, 81, 88 ; nuclear, 81, *83
Spiraea, *594
Spiraeeae, 594
Spiral vessels, 95
Spirillum, *11, 333
Spirochaete, *11, 336
Spirogyra, *347; cell division, *89 ; movements, 267
Spirotaenia, *344
Splint wood, 133
Spongilla, symbiosis with algæ, 234
Spongy parenchyma, *122
Spontaneous generation, 5
Sporangium, 441, *448, 455 ; dehiscence, 448
Spores, 304, 441 ; desiccation, 196
Sporocarps, 451, *453
Sporodinia, *384
Sporogonium, 424, 433, 436
Sporophylls, 38, 441, 458
Sporophyte, 164
Spurge, *Euphorbia*
Spurious fruit, 521
Squill, 543
Stability of the plant body, 178
Stachys, 659
Stalked leaves, 32
Stamen, 37, 475, *502 ; movement of, 296; rate of growth of, 255
Staminodes, 503
Stapelia, 656
Staphisagriae semina, 578
Staphylococcus, 336
Starch, 73, 195 ; assimilation, 73 ; grains, *74, *93 ; grains, action of diastase on, *224 ; grains as statoliths, 274 ; grains, formation in photosynthesis, 218 ; grains, sphæritic structure, 75 ; glutinous, 76 ; reserve, 73 ; sheath, 117, 119 ; transitory, 224
Statice, 649
Statolith theory, 274
Stele, 117
Stellaria, 571
Stellatae, 673
Stem, *117, 118 ; mechanical tissues of, *183 ; of mossplant, 431 ; succulent, 213 ; -tendrils, 27
Stemonitis, *341, 342
Stentor, symbiosis with algæ, 234
Sterculia, buttress roots, *185
Sterculiaceae, 623
Stereome, 182
Stereum, 410
Sticta, 421
Stigma, 505 ; movements of, 296
Stigmatic fluid, 211
Stigmatomyces, *399
Stimulus, 174, 273
Stinging hairs, 105
Stipa, 212, 270 ; leaf, *211
Stipules, 31, 36
Stolons, 25
Stomata, *102, 205, *206, 244 ; development of, 104 ; mechanism of, 206
Stoneworts, Characeae
Stramonii, folia, 663 ; semina, 663
Stratification of cell wall, 65
Stratiotes, 524
Strawberry, *Fragraria*
Streaming of protoplasm, *268, 269
Streptocarpus, 666
Streptochaeta, 527
Streptococcus, 336
Striations of cell wall, *64, 65
Strickeria, *394
Stroma, 395
Strontium in plants, 187
Strophanthi semina, 651
Strophanthus, 651, *653
Structural deviations, 165
Struthiopteris, 446
Strychnine, 226, 649
Strychnos, 649, *652
Style, 505
Styracaceae, 646
Styrax, 646 ; styrax praeparatus, 593
Suberin, 70
Suberised cell walls, 69
Subsidiary cells, 104, 206
Subterranean roots, 47
Succisa, *680
Suction force of transpiring shoots, 205
Sugar, 79, 202 ; -cane, *Saccharum*
Sulphur, 79 ; bacteria, 243, 335 ; in plants, 187, 188, 189
Sumbul radix, 643
Sundew, *Drosera*
Supporting fibres, 82

Surirella, 350
Suspensor, *463, 464
Swarm spores, *55, *265 ; heliotactic movement of, 277
Sweetbay, *Laurus nobilis*
Swertia, 651
Symbiosis, 227, 415
Symmetry, relations of, 15 ; floral, 507
Sympetalae, 645
Symphytum, *513, 658
Sympodium, 18
Synapsis, 84, *85
Syncarpous gynaeceum, 503
Synedra, 350
Synergidae, 514
Syringa, *649

Tabasheer, 192
Tabernaemontana, 652
Tactile hairs, 108 ; pits, *65, 67
Taeniophyllum, 48
Tagetes, 687
Tamarindus, *601, *602, *603, 605
Tamus, 544
Tanacetum, 688
Tannic acid, 563
Tannin, 71, 73, 78, 93, 133
Tapetum, 441
Taphrina, *398
Tap-roots, 47
Taraxaci radix, 688
Taraxacum, 682, *683, *684 ; apogamy, 93, 518 ; tissue tensions, 181
Taxaceae, 489
Taxodium, 494
Taxus, *482, *490, *491 ; vascular system, 124, *125
Tea, 628
Teak, 659
Teazel, *Dipsacus*
Tecoma, 666
Tectona, 659
Teleutospores, 403
Tellurium in plants, 187
Telophase, 84
Temperature, cardinal points of, 176 ; influence on growth, 257
Tendrils, 27, 44, 288, *289 ; climbers, 287
Teratology, 167
Terebinthinae, 610
Tegumentary system, 100
Terminal leaves, 21
Terminalia, 632 ; fruit, 320
Ternstromiaceae, 627
Testudinaria, 544
Tetracyclicae, 649
Tetragonolobus, 607
Tetraspores, 375
Teucrium, 659
Thalictrum, 574 ; apogamy, 93, 518
Thallium in plants, 187
Thallophyta, 110, 329 ; conducting tracts, 110 ; form, 11 ; fossil, 465
Thallus, 11
Thamnidium, 385
Thea, *628
Theine, 226
Thelephora, *417
Thelephoreae, 410
Theobroma, *624, *625, 626
Theobromine, 226
Thermotropism, 286
Thesium, 231, 644 ; haustoria, 49
Thladiantha dubia, 249
Thlaspi, 591
Thornapple, *Datura*
Thorns, 28
Thuja, 492 ; germination, *161
Thus americanum, 498
Thymelaeaceae, 631
Thymelaeinae, 631
Thymol, 660
Thymus, 660
Tilia, 623, *624 ; bast, *141 ; stem, *138 ; wood, *138, *139, *140
Tiliaceae, 623
Tillandsia, 49, 197, 213
Tilletia, 402, *403
Tilletiaceae, 402
Tin in plants, 187
Tissues, 97 ; mechanical, 182, *183 ; primary, 100 ; secondary, 100, 127 ; systems, 99 ; tension of, 181
Titanium in plants, 187
Tobacco, 663
Tolypellopsis, 365
Tomato, *Lycopersicum*
Tonoplast, 58
Toothwort, *Lathraea*
Tozzia, 231, 666
Tracheae, 35, 95
Tracheides, 72, 96, 112, *132, *135 ; fibrous, 72, 135 ; vascular, 72
Traction fibres, 82
Tradescantia, cell, *59 ; circulation of protoplasm, 59 ; direct division, *87 ; hairs, 107 ; stomata, *103
Tragacantha, 609
Tragopogon, 682
Transfusion cells, 120
Transition cells, 115
Transitory starch, 224
Transpiration, 196, 205-209, 212 ; current, *202 ; current, causes of, 203
Transverse heliotropism, 277
Trapa, 42
Trees, 29 ; age of, 263 ; ferns, 445, *446 ; ferns adventitious roots, 48 ; influence of wind on, *177 ; weeping varieties, 29, 251
Tremella, *400
Tremellineae, 408

Trentepohlia, 357
Trichia, *342
Trichocaulon, 656
Trichogyne, 376, *377, 388, 419
Trichomanes, *449
Trichomes, 105 ; internal, 116
Tricoccae, 615
Trifolieae, 607
Trifolium, 607 ; movements, 293 ; stipules, 36
Triglochin, 224
Trigonella, 607
Triplaris, 235
Triplocaulescent, 28
Triticum, *527, *528 ; aleurone, *77
Tropaeolaceae, 610
Tropaeolum, 610 ; cell, *63 ; exudation, *209 ; heliotropism, 277 ; leaf, 43, *209 ; water stomata, *105
Trophoplasm, 59
Tropic curvatures, 270
Truffles, 397
Tsuga bud, *39
Tuber, *25
Tuber, *396, 397
Tuberaceae, 397
Tubiflorae, 656
Tubuliflorae, 681
Tulip tree, *Liriodendron*
Tulipa, *24, 541
Turgidity, 178
Turgor, movements due to, 291
Tussilago, *686, 688
Twining plants, 30, 281
Tylosis, *133
Typhaceae, 530

Ulex, 607
Ullmannia, 501
Ulmaceae, 563
Ulmus, *31, *515, 563, *564 ; adventitious shoots, 20 ; leaf, *31
Ulothrix, *92, 357, *358
Ulotrichales, 357
Ulva lactuca, *12
Umbel, 509, *510, *511
Umbelliferae, 636 ; oil ducts, 98
Umbelliflorae, 635
Uncaria, 673
Uncinula, 390, *391
Uniaxial, 28
Unicellular hairs, 107
Upper leaf, 31
Uragoga, 672, 673, *674
Uredineae, 403
Uredospores, 407
Urginea, *540, 541
Urtica, 566 ; hybridisation, *315 ; stinging hairs, 105, *106
Urticaceae, 566
Urticinae, 563
Usnea, 418
Ustilagineae, 401
Ustilago, *401 ; basidium, *402
Utricularia, 49, 97, 237, 668 ; bladder, 43 ; leaf, 43, *44
Uvae, 623
Uvae ursi folia, 646

Vaccineae, 646
Vaccinium, *645, 646
Vacuoles, 53 ; contractile, 56
Valerian, *Valeriana*
Valeriana, 675, *676
Valerianae rhizoma, 675
Valerianella, 675
Vallisneria, 21, 524
Valvate leaves, 38
Vanilla, *549
Vanillin, 70, 226
Variation, external causes of, 165 ; fluctuating, 3 ; in hybrids, 316 ; movements, 291
Vascular, bundles, 111 ; system, 100, 109 ; closed, 113 ; termination of, *116
Vascular cryptogams, *Pteridophyta*
Vascular plants, 154
Vascular tracheides, 72, 135
Vaucheria, 361, *362
Vegetable ivory palm, *Phytelephas*
Vegetative, cone, 18 ; reproduction, 297, 300
Veins, 34
Velamen, 48, 120 ; radicum, 109
Velum, 412
Venation, 34, 110
Ventilating system, 98
Venus' Fly-trap, *Dionaea*
Veratrine, 226
Veratrinum, 543
Veratrum, 543
Verbascum, 33, 664, *667
Verbena, 657, 659
Verbenaceae, 658
Vernation, 38
Veronica, 213, 665 ; *cupressoides*, *212
Verrucaria, 418
Vessels, 95 ; pitted, 95 ; reticulate, 95 ; scalariform, 95, *96 ; spiral, 95
Vibrio, *333, 336
Viburnum, 674
Vicia, *604, 609 ; geotropism, *281 ; growth, 257 ; root tubercles, *231
Vicieae, 609
Victoria regia, heat produced by respiration, 244
Vinca, 651, *655 ; sclerenchymatous fibre, *64
Vincetoxicum, 654, *655
Vine, *Vitis*
Viola, *188, *507, *519, *629, 630 ; emergences, 107, *108 ; papillae, *105

Violaceae, 629
Violet, *Viola*
Viscaria, *569
Viscum, *94, 231, *644 ; epidermis, 146 ; false dichotomy, 18
Vitaceae, 623 ; aluminium, 192
Vital force, 174
Vital properties of plants, 172
Vitis, *622, 623 ; tendrils, 27
Vittae, 98
Voltzia, 501
Volva, 412
Volvocales, 353
Volvox, *354, 355

Walchia, 500
Walking fern, *Camptosorus rhizophyllus*
Water, absorption of, 197 ; constitution, 196 ; -culture, *190 ; distribution of, 200 ; exudation of, 209 ; imbibition, 194 ; necessary for assimilation, 219 ; -plants, 245 ; -plants, growth in air and water, 260 ; -stomata, 104 ; *105, 123 ; -supply, regulation of, 212
Water Crowfoot, *Ranunculus aquatilis*
Water-ferns, Hydropterideae
Water Hemlock, *Cicuta*
Water-net, *Hydrodictyon utriculatum*
Water Parsnip, *Sium*
Water-pores, water-stomata
Wax, *101
Weigelia, 675
Welwitschia, 498
Wheat, *Triticum*
White Thorn, *Crataegus*
Willoughbeia, 651
Willow, *Salix*
Willow-herb, *Epilobium*
Winter buds, 109
Witches'-brooms, 398
Wolffia, 49, 197, 536
Wood, autumn, 131 ; elements, *137 ; fibres, 134, 136 ; parenchyma, 134, 140 ; secondary, 134 ; spring, 131
Woodruff, *Asperula*
Wormwood, *Artemisia*
Wounds, healing of, 150

Xanthein, 80
Xanthophyll, 62, 63
Xanthoprotein, reaction, 57
Xanthoria, *416, *417
Xenia, 305
Xerophytes, 212 ; stomata of, 104
Xylem, 111, 112 ; parenchyma, 112
Xylochrome, 133

Yam, *Dioscorea*
Yew, *Taxus baccata*
Yucca, *511, 543 ; pollination, 308 ; thickening, 144

Zamia, 485, *487, *488 ; spermatozoid, *487
Zanichellia, 524
Zea, 528 ; bundles, *110, *111 ; exudation of water from, 209 ; stem, *117
Zinc in plants, 187
Zingiber, 546, *547 ; ethereal oil, 79
Zingiberaceae, 456
Zinnia, 687
Zostera, 524 ; pollination, 307
Zygnemaceae, 346
Zygomorphic, flowers, *508 ; symmetry, 16
Zygomycetes, 383
Zygophyllaceae, 611
Zygosaccharomyces, 399
Zygospore, 331, 344, 384, *385
Zymase, 223

THE END

Printed by R. & R. CLARK, LIMITED, *Edinburgh*.

8vo. 18*s. net.*

THE ORIGIN OF A LAND FLORA

A THEORY BASED UPON THE FACTS OF ALTERNATION

BY

F. O. BOWER, Sc.D., F.R.S.

REGIUS PROFESSOR OF BOTANY IN THE UNIVERSITY OF GLASGOW

With numerous Illustrations.

In his Preface the author explains that his interest in the question discussed in the present work has been of long standing; that it seemed to him probable that some biological cause had determined the prevalence and constancy of the alternation, to which apogamy and apospory appear as occasional exceptions. The theory was entertained that the change of conditions involved in the invasion of the land by organisms originally aquatic had played a prominent part in the establishment of those alternating phases of the life-cycle which are so characteristic of Archegoniate plants. As early as 1890 Professor Bower briefly stated his theory in a paper published in the *Annals of Botany*, but his researches have led him to the conclusion that only "now, after the lapse of seventeen years, it has been possible to state the biological argument more fully in the present volume, strengthened by many new facts. The first part deals with the general theory. The second part is taken up with a detailed statement of the facts, together with comparison of the constituents of the several phyla *inter se.* The third part is devoted to general comparisons and conclusions. . . .

"The attempt has been made to work in the results of Palæontological research with those of the comparative analysis of living forms. The enquiry has related to all the characters, both vegetative and propagative, of the sporophyte generation: these include the external form, the embryogeny, and anatomical features, and especially the structure and development of the spore-producing members, while the characters of the gametophyte have also been taken into account. It is found that the conclusions arrived at are supported by general convergence of the lines of evidence derived from all of these sources."

Professor Bower's important work is a substantial volume of over seven hundred pages, with a large number of illustrations.

MACMILLAN AND CO., Ltd., LONDON.

WORKS ON BOTANY

THE STUDENT'S FLORA OF THE BRITISH ISLANDS. By Sir J. D. Hooker, M.D., D.C.L., LL.D., F.R.S. Third Edition. Globe 8vo. 10s. 6d.

BOTANICAL TEXT-BOOK. Vol. I. Structural Botany; or, Organography on the Basis of Morphology. To which is added the Principles of Taxonomy and Phytography, and a Glossary of Botanical Terms. By Asa Gray, LL.D., Fisher Professor of Natural History (Botany) in Harvard University. 8vo. 10s. 6d. Vol. II. Physiological Botany. I. Outline of the History of Phaenogamous Plants. II. Vegetable Physiology. By G. L. Goodale. 8vo. 10s. 6d.

TIMBER AND SOME OF ITS DISEASES. By H. Marshall Ward, D.Sc., F.R.S., F.L.S., formerly Professor of Botany in the University of Cambridge. Illustrated. Crown 8vo. 6s.

DISEASE IN PLANTS. By Dr. H. Marshall Ward. Crown 8vo. 7s. 6d.

LECTURES ON THE EVOLUTION OF PLANTS. By Douglas Houghton Campbell, Ph.D., Professor of Botany in the Leland Stanford Junr. University. Crown 8vo. 4s. 6d. net.

UNIVERSITY TEXT-BOOK OF BOTANY. By Professor Douglas Houghton Campbell. 8vo. 17s. net.

THE STRUCTURE AND DEVELOPMENT OF MOSSES AND FERNS. (*Archegoniatae*). By Professor Douglas Houghton Campbell. 8vo. 18s. 6d. net.

NOTES ON THE LIFE-HISTORY OF BRITISH FLOWERING PLANTS. By Lord Avebury. Illustrated. 8vo. 15s. net.

MACMILLAN AND CO., Ltd., LONDON.